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Phenology and biology of harvestmen in and near Sapporo, Hokkaido, Japan, with some taxonomical notes on *Nelima suzukii* n. sp. and allies (Arachnida: Opiliones)

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Abstract — Phenology and biology of a total of 11 opilionid species were surveyed in and near Sapporo, Hokkaido. Most of the species showed an annual life cycle with overwintering in egg stage. Exceptions were *Paraumbogrella pumilio* having an annual cycle with adult hibernation and *Sabacon makinoi* with overwintering in both egg and juvenile stages. Compared to the phenological patterns of opilionid assemblage in Shikoku, southwestern Japan, those in Hokkaido were characterized by the absence of species with overwintering in juvenile stage. Among the species overwintering as eggs, species whose juveniles emerge earlier in spring tended to have longer juvenile period. Furthermore, in most of the species females reached adulthood earlier than males (protogyny). The protogyny seems to be rather prevalent in harvestmen of the superfamily Phalangioidea including Phalangiidae and Sclerosomatidae, although it has been only rarely documented in insects and other arachnids. Long reproductive period and multiple mating by females connected with presumable last sperm precedence might explain protogeny in harvestmen. Except for three soil-dwelling species (*Sabacon makinoi, S. imamurai*, and *Paraumbogrella pumilio*), all species changed their diurnal microhabitat preference from soil litter on the ground to upward herbaceous layer or tree trunks before they reach adulthood. Even in sexually reproducing species, adult sex ratios in the field often deviated from 1: 1. Relative abundance between male and female changed also temporally, probably as a result of sexual difference in microhabitat preference and in reproductive behavior. Data on fecundity of some species and egg size of ten species were presented. Mucous egg sacs produced by two *Sabacon* species are described and illustrated for the first time. In addition, a new name *Nelima suzukii* is proposed for one of the two species of the genus *Nelima*, with some notes on their taxonomy and biology.

Key words — life cycle, phenology, protogyny, sex ratio, thelytoky, Opiliones, *Nelima suzukii* n. sp.

Introduction

Harvestmen are relatively huge and abundantly found invertebrates in various types of forests in the world and the English name "harvestmen" means creatures most frequently found in the harvest season, late summer or fall (Shear 1982; Hillyard & Sankey 1989). Their phenology has gained attention and several surveys have been conducted mainly in Europe and North America (Stipperger 1928; Pfeifer 1956; Meinertz 1964; Slagsvold 1976; Meijer 1972, 1984; Rambla 1985; Gruber 1996 in continental Europe / Todd 1949; Phillipson 1959; Williams 1962; Curtis 1973 in Great Britain / Martens 1993 in Himalaya / Edgar 1971; Cokendolpher et al. 1992 in North America). However, only fragmental knowledge has been accumulated for the biology and ecology of Japanese harvestmen (Miyosi 1941, 1942, 1944; Tsurusaki 1986), although their role as predators in the forest ecosystem cannot be disregarded in Japanese Islands.

In order to confirm the seasonal trends of life cycles of various opilionid species, I engaged in a series of periodical field surveys at three sites, Maruyama, Nopporo, and the Campus of Hokkaido University, all located in and near Sapporo, Hokkaido in 1979. Of these, results of the surveys on two thelytokous species, *Leibunum manubriatum* and *L. globosum* were already reported (Tsurusaki 1986). Here I will present results on all the remaining species and discuss general trend of life cycles and hibernation stages of harvestmen. Furthermore, I will also present some biological data on the two closely related species of the genus *Nelima*: *N. genufusca* and *N. suzukii* n. sp., together with some notes on taxonomy of Japanese *Nelima* species.

Areas Surveyed and Methods

Periodical surveys were carried out in the daytime from late spring to November in 1979, when the forest grounds

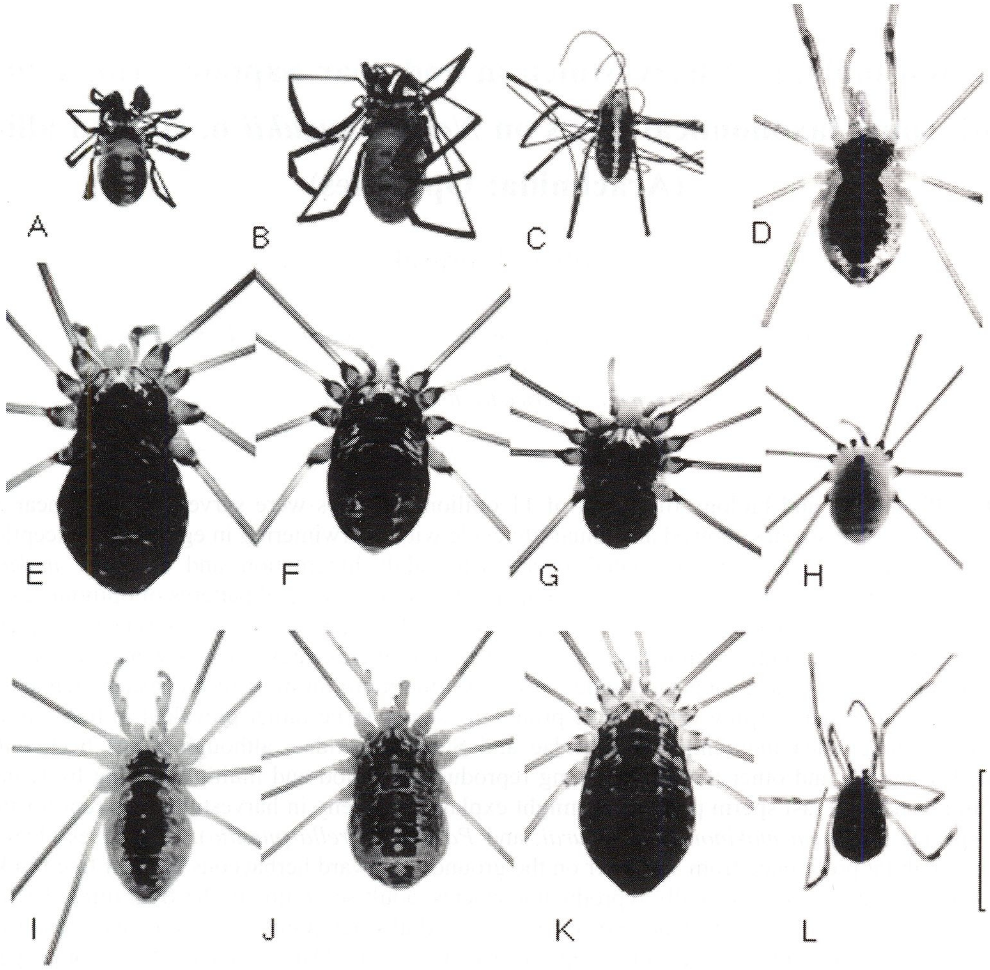


Fig. 1. Eleven species of harvestmen surveyed in Maruyama, Nopporo, and Campus of Hokkaido University. A, *Sabacon makinoi*; B, *S. imamurai*; C, *Caddo agilis*; D, *Odiellus aspersus*; E, *Nelima genufusca*; F-G, *N. suzukii* n. sp.; H, *Leiobunum japonicum*; I, *L. manubriatum*; J, *L. globosum*; K, *Psathyropus tenuipes*; L, *Paraumbogrella pumilio*. Except for male *N. suzukii* (G), all the specimens are females. All the photos to scale. Scale=5 mm.

Table 1. Opilionid species collected at Maruyama, Nopporo and the campus of Hokkaido University in 1978–1979. +: recorded. −: not recorded. *: Only one male was collected on September 12, 1979.

Species	Maruyama	Nopporo	University Campus
Family Caddidae			
Caddo agilis Banks 1892	−	+	−
Family Phalangiidae			
Odiellus aspersus (Karsch 1881)	+	+	+
Family Sclerosomatidae			
Subfamily Leiobuninae			
Leiobunum japonicum Müller 1914	+	+*	+
Leiobunum manubriatum Karsch 1881	+	+	−
Leiobunum globosum Suzuki 1953	+	+	−
Nelima genufusca (Karsch 1881)	+	+	+
Nelima suzukii n. sp.	+	+	−
Subfamily Gagrellinae			
Psathyropus tenuipes L. Koch 1878	+	−	+
Paraumbogrella pumilio (Karsch 1881)	−	+	+
Family Sabaconidae			
Sabacon makinoi makinoi Suzuki 1949	+	+	−
Sabacon imamurai Suzuki 1964	+	+	−

are free from snow coverage. The opilionid species collected from the three areas surveyed are listed in Table 1 and shown in Fig. 1. Of the 14 species so far recorded from Hokkaido (Suzuki & Tsurusaki 1983), 11 were collected in the present survey. I chose three localities (Maruyama, Nopporo, and the Campus of Hokkaido University), situated at relatively low altitudes in and near Sapporo, Hokkaido as survey areas (Fig. 2). Phenological survey of ten species was made at Nopporo or Maruyama or both, while that of remainder, *Paraumbogrella pumilio*, was studied at the Campus of Hokkaido University. Topographic condition and vegetation of each survey area and sampling procedures are as follows:

A) Maruyama: Weekly line census was performed along a path penetrating a deciduous, broad-leaved forest (mainly *Cercidiphyllum japonicum, Acer mono*, and *Quercus mongolica*) and an afforestation area of the Japanese Red Cedar (*Cryptomeria japonica*), which are situated at the western outskirts of Mt. Maruyama. Main undergrowth consisted of several species of annual plants (*Heracleum lanatum, Corydalis ambigua, Achyranthes bidentata, Laportea bulbifera*, etc.). All individuals of Opiliones found on the ground, herbaceous layer, tree trunks, or stone monuments or stone lanterns around Daishi-do Shrine were collected by hand, walking along the regular course of about 700 m for more than 90 min. Litter layer, debris and logs, and the bases of herbs were carefully examined in order to collect young individuals of every species. Collected specimens were preserved in vials containing 80% ethanol separately according to the types of microhabitats at collection sites (ground, herbaceous layer, tree trunks, and stone monuments) so as to examine their microhabitat preference.

B) Nopporo: Similar weekly collecting was carried out at Nopporo Natural Forest (about 90 m alt.), situated at about 15 km east of the center of Sapporo city. The area surveyed consisted of several kinds of deciduous broad-leaf forests (*Cercidiphyllum japonicum, Ulmus davidiana, Kalopanax pictus, Fraxinus lanuginose*, etc.) and plantations of Sakhalin fir (*Abies sachalinensis*), with bamboo grass (*Sasa kurilensis*), as main undergrowth. Annual herbaceous plants found along the trails included *Heracleum dulce, Eupatorium glehni, Trillium kamtschaticum, Cardiocrinum cordatum, Impatiens noli-tangere* and so on. The survey covered a rather broad area and spent enough time (more than two hours), since population density of each species in this area was relatively low. Harvestmen were collected separately depending on their microhabitats (ground, herb, or tree trunks) and preserved in 80% ethanol.

C) Campus of Hokkaido University: Phenology of *Paraumbogrella pumilio* was studied at an open meadow adjacent to the farm situated in the University campus, the center of Sapporo city. Although occurrence of some other species of Opiliones was confirmed in the nearby forest, only one male of *Psathyropus tenuipes* was found in the study area. A 60-minute census by hand with a pooter was performed every two weeks.

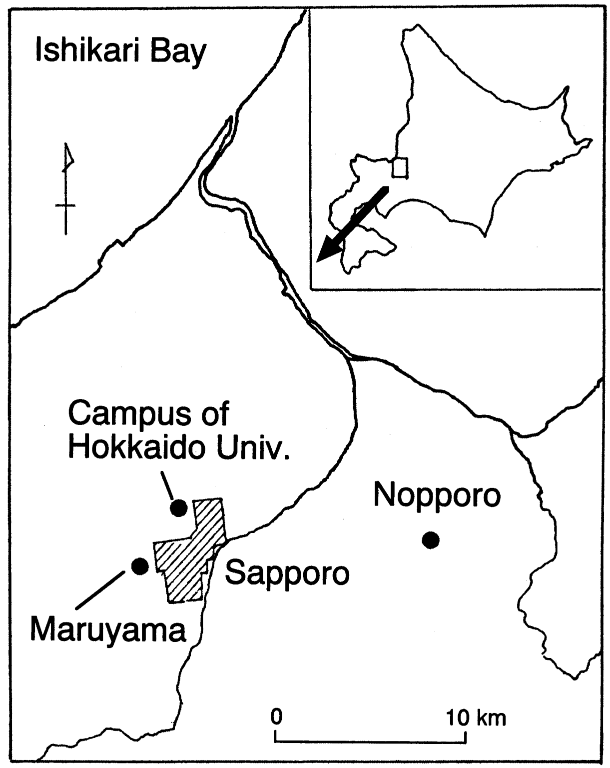


Fig. 2. Locations of the areas surveyed.

The above three survey areas studied were covered with snow from late November to mid April with a maximum depth of about 1 m. Mean monthly temperature and maximum depth of snowfall at the Sapporo Meteorological Station close to Maruyama and the Campus of Hokkaido University and those at the Nishi-Nopporo Meteorological Station adjacent to Nopporo are shown in Fig. 3 (Sapporo Weather Station 1979).

Females of two *Nelima* species collected from Nopporo were dissected and the state of ovarian development and the number of mature eggs retained in the egg reservoir (=uterus internus; usage of the term "egg reservoir" see Tsurusaki 1982) were examined. Ovarian conditions were classified into four stages: Stage I (immature ovary) — whole the ovary is aciniform with no accumulation of yolk; Stage II — at least some egg cells started to accumulate yolk but not yet mature; Stage IIIa — mature eggs are retained in ovary, not in the egg reservoir; Stage IIIb — mature eggs are retained in both ovary and the egg reservoir. When experience of oviposition was clearly inferred from the wrinkles of skin at lateral sides of her body, the female was assigned to stage IIIb even if no mature eggs were present.

To estimate number of eggs laid, female adults of seven species at the pre-reproductive stage were reared in the laboratory. *Paraumbogrella pumilio* was reared in petri dishes (8.5 cm inside diameter and 5.5 cm high) with soil of about 15 mm thickness at the bottom. For other six species, plastic containers (24 cm i.d. × 12 cm high) or unglazed flower pots (20 cm i.d. × 19 cm high) were used for rearing.

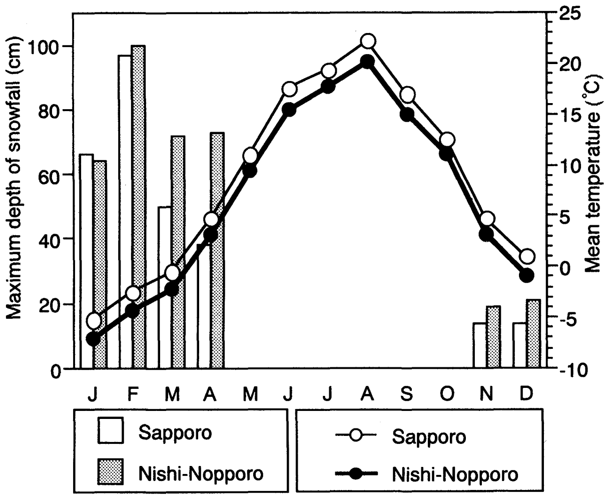


Fig. 3. Mean temperature and maximum depth of snowfall at the Sapporo Meteorological Station and the Nishi-Nopporo Meteorological Station in 1979 based on data provided by Sapporo Weather Station (1979).

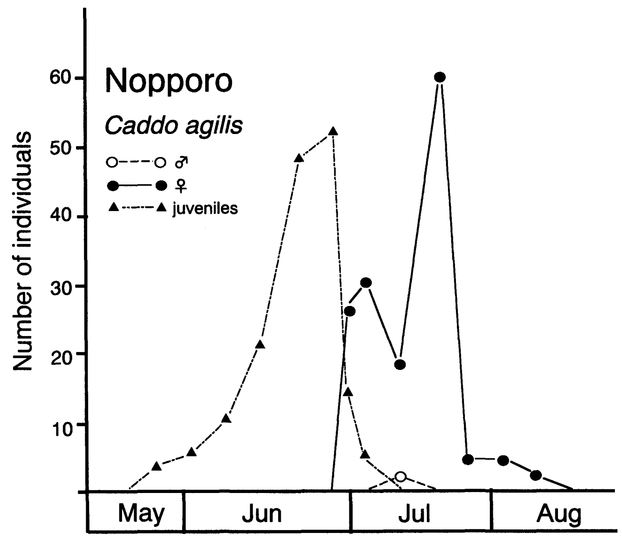


Fig. 4. Seasonal fluctuation in the number of individuals of *Caddo agilis* in Nopporo in 1979.

Soil was laid with appropriate thickness (3 to 4 cm for a plastic container). A female and a male collected in the field prior to reproductive season were kept in each container. When eggs laid were discovered, they were dug out from the soil and then returned to the original places after counting the number of eggs and measuring the lengths of major and minor axes of eggs. When females died during the rearing, the size of mature eggs stored in egg reservoir of females were also measured by dissecting the females.

Results

1. Phenology

Figures 4–8 show the seasonal fluctuation in number of individuals of collected through the periodical surveys in 1979. Some notes are presented for each species:

Caddo agilis (Caddoidea: Caddidae) (Fig. 4). This species was only found in Nopporo during the 1979 surveys, though occurrence of the species in Maruyama was ascertained later (2 females found on tree trunks on 4 July 1980). First juveniles were found on 21 May in soil litter. Female adults appeared from 30 June and culminated in number in mid July. Only two males were collected throughout the survey, as was already reported in Suzuki & Tsurusaki (1983). To ascertain parthenogenesis, I tried to rear several penultimate females in the laboratory in 1979. It failed, however, since they accepted none of the foods such as cheese, sausages, bread, or dead insects. Since other species of harvestmen immediately consume these food when they were provided, it is very likely that *Caddo agilis* is a genuine predator. Unlike other species of harvestmen the second legs of *Caddo agilis* are not the longest and are not used for antennal sensor. Having a suite of traits suitable for prey capture such as highly developed huge eyes, agile movement, and raptorial palps with three large ventral spines on each of the femora, supports the possibility as an able predator.

Odiellus aspersus (Phalangiidae: Oligolophinae) (Fig. 5). This species was formerly treated under the name "*Oligolophus aspersus*". Although detailed taxonomic revision has not been conducted yet, I treat this species under the genus *Odiellus* according to Staręga (1978). First juveniles emerged 10 May and 14 May in Maruyama and Nopporo, respectively. Female adults begun to emerge in early August about one week earlier than males in both localities.

Leiobunum manubriatum and *L. globosum* (Screlosomatidae: Leiobuninae). Phenologies of these thelytokous species were already reported in Tsurusaki (1986).

Leionubum japonicum (Screlosomatidae: Leibonuninae) (Fig. 5). This species tends to inhabit secondary forests. Except for one male collected on 12 September, no specimens of this species were found during the survey in Nopporo. First juveniles were found in early June and molted to adults in early August in Maruyama.

Psathyropus tenuipes (Screlosomatidae: Gagrellinae) (=*Metagagrella tenuipes* in Suzuki & Tsurusaki 1983, for the usage of the name, see Crawford 1992) (Fig. 5). This species shows synanthropic propensity and are usually found in parks with lawns and groves in northern Japan (Tsurusaki, 1993). In Maruyama, a population of this species was established only in a highly limited area around a small shrine (Daishi-do) situated at the entrance of a climbing trail to top (256 m in alt.) of Mt. Maruyama. Juveniles appeared in early June and molted to adults from late July to late August.

Nelima genufusca (Sclerosomatidae: Leiobuninae) (Fig. 6). This species (="*N. gigantea*" in Suzuki & Tsurusaki, 1983) and the next species, *N. suzukii* n. sp. (= "*N. genufusca*" in Suzuki & Tsurusaki, 1983) are two

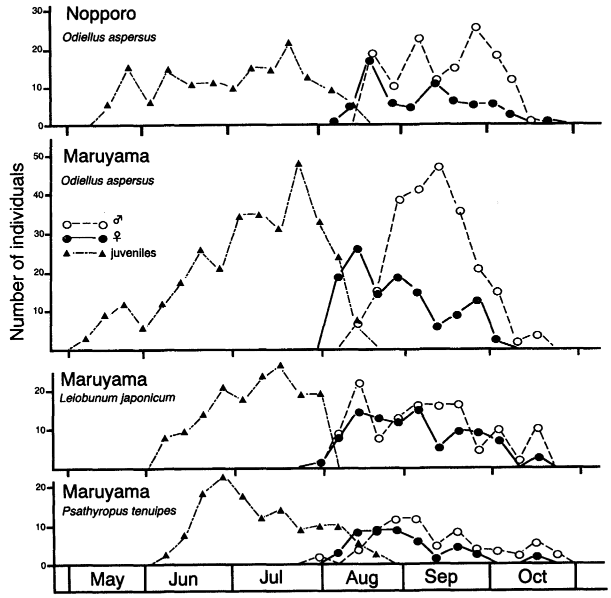


Fig. 5. Seasonal fluctuation in the number of individuals of *Odiellus aspersus, Leiobunum japonicum*, and *Psathyropus tenuipes* in Maruyama and Nopporo in 1979.

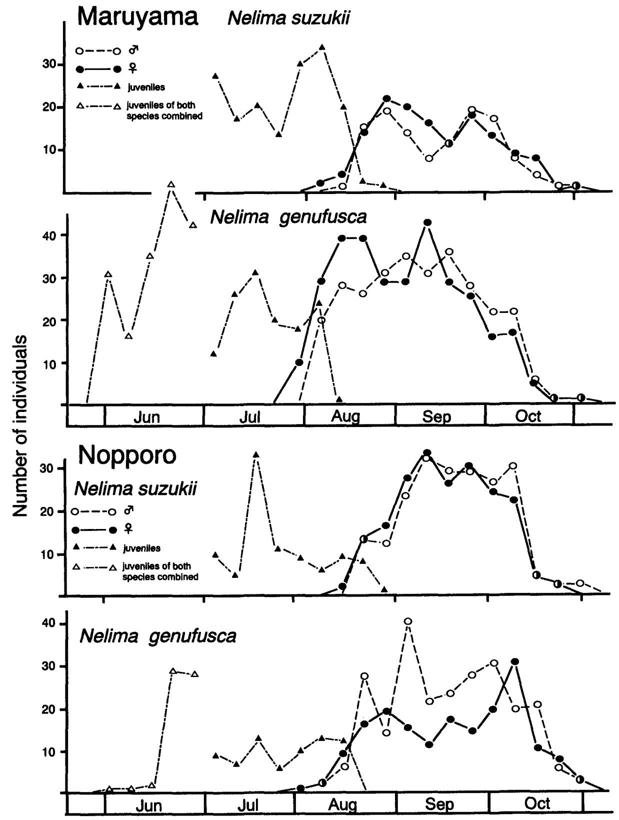


Fig. 6. Seasonal fluctuation in the number of individuals of *Nelima genufusca* and *N. suzukii* n. sp. in Maruyama and Nopporo in 1979. Juveniles of both species collected in June were combined, because their accurate identification was impossible.

commonest species throughout Hokkaido. They look extremely similar to one another, though their bodies are distinctively different in size (Suzuki & Tsurusaki 1983, also see Fig. 1 E-G). Due to this extreme similarity, species identification was not possible for juveniles in younger stages, though it is likely that first juveniles appeared in early June were of *N. genufusca*. First adults of *N. genufusca*, which were all females, emerged around the end of July or the beginning of August.

Nelima suzukii (Sclerosomatidae: Leiobuninae) (Fig. 6). Juveniles of the species attained adulthood in mid August, which was 1 or 2 weeks later than that of *N. genufusca*. Except for this difference, durations of adult stage completely overlapped in the two species.

Sabacon makinoi (Ischyropsalidoidea, Sabaconidae) (Fig. 7). This species, with adult body length of about 2.5 mm, is a soil dweller and usually found beneath stones or logs. Adults were found throughout the year, though they were most abundant in October to early November. Occurrence of juveniles was also scattered all the year round. Egg sacs were found from July to November (see Section 6).

Sabacon imamurai (Ischyropsalidoidea: Sabaconidae) (Fig. 7). This species is larger than the former species (body length: ca. 3 mm). Juveniles of the species were always easily distinguished from *S. makinoi* by 1) having relatively slender body with longer legs and by 2) having legs with longer hairs. Juveniles were observed from April to August, while appearance of adults were limited to September and October.

Paraumbogrella pumilio (Fig. 8) (Sclerosomatidae: Gagrellinae). This species of about 3 mm in adult body size is also epigeal and usually found on ground under turf grasses, under stones or logs on forest ground, and occasionally on herb. Juveniles of the species appeared from mid June and completely disappeared in early October, whereas adults were found all year round with the peak of numbers in September. Most of the adults found in September and October showed apparently brighter coloration than those in spring, and the brighter individuals can safely be considered as post-hibernating adults. During the laboratory rearing of eight pairs of a female and a male from 7 May to 14 August 1979, oviposition took place from mid May to mid June. Those females had slim abdomens when the rearing started. Ovary was still in the process of development when a female was dissected in 7 May.

2. Emergence order of juveniles and adults

Concerning nine species which hibernate as eggs, dates of the first and the last observations of juveniles and adults are given in Table 2. Since these periodical surveys were carried out once a week, the comparison among the species has the limit to some extent. However, some tendencies can be pointed out.

Emergence order of juveniles: Juveniles of *Sabacon imamurai* were found in the earliest time in spring.

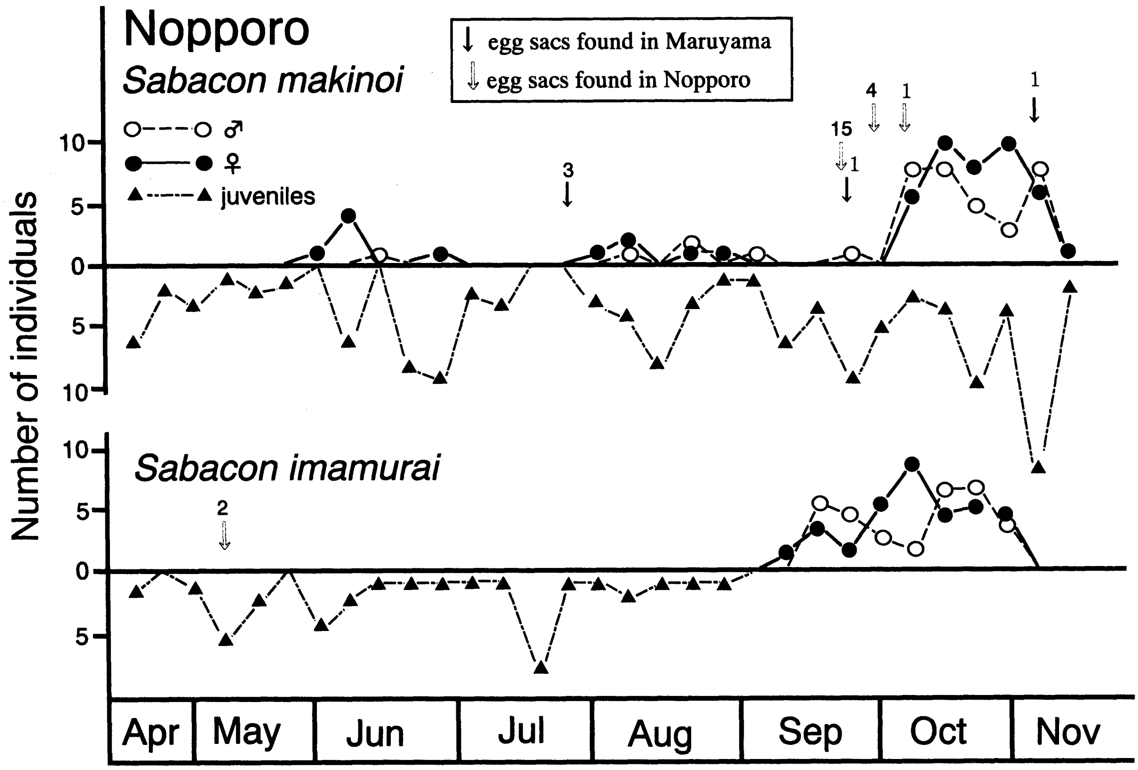


Fig. 7. Seasonal fluctuation in the number of individuals of *Sabacon makinoi* and *S. imamurai* in Nopporo in 1979.Times discovering egg sacs in Nopporo and Maruyama and the number of egg sacs observed are also shown in arrows and numerals, respectively.

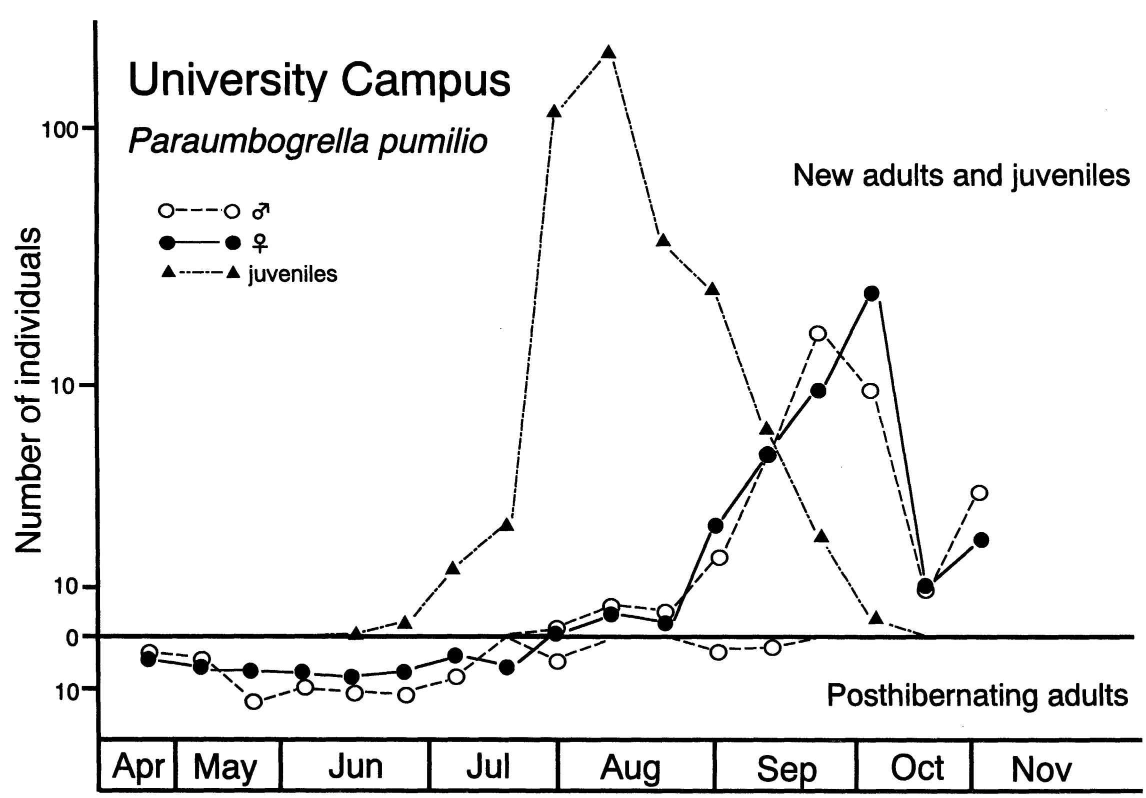


Fig. 8. Seasonal fluctuation in the number of individuals of *Paraumbogrella pumilio* in the campus of Hokkaido University in 1979.

Table 2. The date (month/day) of the first and the last observations of juveniles and adults of nine species at Maruyama and Nopporo in 1979 and approximate duration (days) of juvenile and adult stages.

Species	First observation			Last observation		Duration (days)		
	juv.[1)]	female	male	juv.	adult	juv.	adult	total
Maruyama								
O. aspersus	5/10	8/6	8/13	8/13	10/17	88	65	153
L. japonicum	6/7	7/30	8/6	8/13	10/17	53	65	118
L. manubriatum	(5/1)	7/10	–	8/6	10/3	(70)	58	(128)
L. globosum	(5/1)	7/6	–	7/17	9/26	(66)	71	(137)
N. genufusca	(6/1)	7/30	8/6	8/13	11/1	(59)	80	(139)
N. suzukii	(6/1)	8/6	8/13	8/29	11/1	(66)	63	(129)
Ps. tenuipes	6/7	8/6	7/30	8/22	10/26	60	65	125
Nopporo								
Caddo agilis	5/21	6/30	7/9	7/5	8/8	40	34	74
O. aspersus	5/14	8/8	8/21	8/14	10/25	86	72	158
L. manubriatum	(5/2)	7/26	–	7/28	9/25	(85)	59	(144)
L. globosum	(5/2)	7/12	7/20	7/28	10/2	(71)	66	(137)
N. genufusca	(6/2)	8/3	8/8	8/14	10/13	(62)	78	(140)
N. suzukii	(6/2)	8/14	8/21	8/28	10/31	(73)	64	(137)
S. imamurai	4/20	9/12	9/20	8/28	10/31	145	64	209

[1)] Species identification of the following two pairs was impossible in the younger juvenile stages because of extremely similar forms: *Leiobunum manubriatum* / *L. globosum* and *Nelima genufusca* / *N. suzukii*. Hence dates and durations in parentheses cannot be decided precisely.

Probably juveniles of this species hatched out as soon as the thawing takes place. Combining the two species pairs whose identification is impossible at younger juvenile stage, emergence of juveniles of the nine species can be arranged in the following order: *Sabacon imamurai* > *Leiobunum manubriatum* + *L. globosum* > *Odiellus aspersus* > *Caddo agilis* > *Nelima genufusca* + *N. suzukii* > *L. japonicum* = *Psathyropus tenuipes*.

Emergence order of adults: The adult emergence of *Caddo agilis* was remarkably earlier than the others. *Leiobunum globosum* and *L. manubriatum* followed *Caddo agilis*. It is interesting that adults of such parthenogenetic species emerge in relatively earlier season. The adult emergence of the remaining species concentrated in early August except for *Sabacon imamurai*, which matured in September. In closely related species such as *Leiobunum globosum* and *L. manubriatum* or *Nelima genufusca* and *N. suzukii*, a slight difference in their adult emergence was detected. Namely, *Leiobunum globosum* preceded *L. manubriatum* one week or less (see Tsurusaki 1986), and *Nelima genufusca* preceded *N. suzukii* about one or two weeks (Fig. 6). Precedence of female emergence in adult stage was observed in all species that reproduce bisexually, except for *Psathyropus tenuipes*.

Length of juvenile period: Caddo agilis was outstanding in extremely short growth period. On the contrary, juvenile period of *Sabacon imamurai* seems exceedingly long. Although length of juvenile period was more or less similar in other seven species belonging to the superfamily Phalangioidea, there was a tendency that species which emerge in earlier season grow more slowly (Fig. 9). The date of first observation of juveniles was significantly correlated with the length of juvenile period in the seven species (Kendall's coefficient of rank correlation $\tau=0.75$, $p=0.02$). The significance was also observed even when two non-Phalangioidea species, *Sabacon imamurai* and *C. agilis* were included in the analysis ($\tau=0.588$, $p=0.03$).

Length of adult period and life span: The adult period of *C. agilis* was also exceedingly short, accordingly this species seems to have very short postembryonic life span. The difference in length of adult among other species was not so large. Disappearance of adults of *L. manubriatum* and *L. globosum*, as well as two species of *Nelima*, took place nearly simultaneously, though dates of adult emergence of these closely related species were somewhat different with each other.

In conclusion, phenology of the nine species with hibernation in egg stage seems to differ at the level of family or superfamily and the general trends are summarized as follows: 1) Short juvenile and short adult periods: *C. agilis* (Caddidae), 2) Long juvenile and long adult period: *S. imamurai* (Sabaconiidae), 3) Medium juvenile and long adult period: other species (Phalangioidea: Phalangiidae and Screlosomatidae).

3. Microhabitat preference

Of the eleven species surveyed, three species, *Sabacon makinoi*, *S. imamurai*, and *Paraumbogrella pumilio* were consistently found on the ground alone. In the other eight species, transition of microhabitat from soil litter to upper layers such as herbs or tree trunks was observed (Figs. 10–11, For *Leiobunum manubriatum* and *L. globosum* see Tsurusaki 1986). In those figures, relative frequencies in each pie chart were obtained by summing the collection data bimonthly.

In *Caddo agilis*, juveniles were found at ground only in

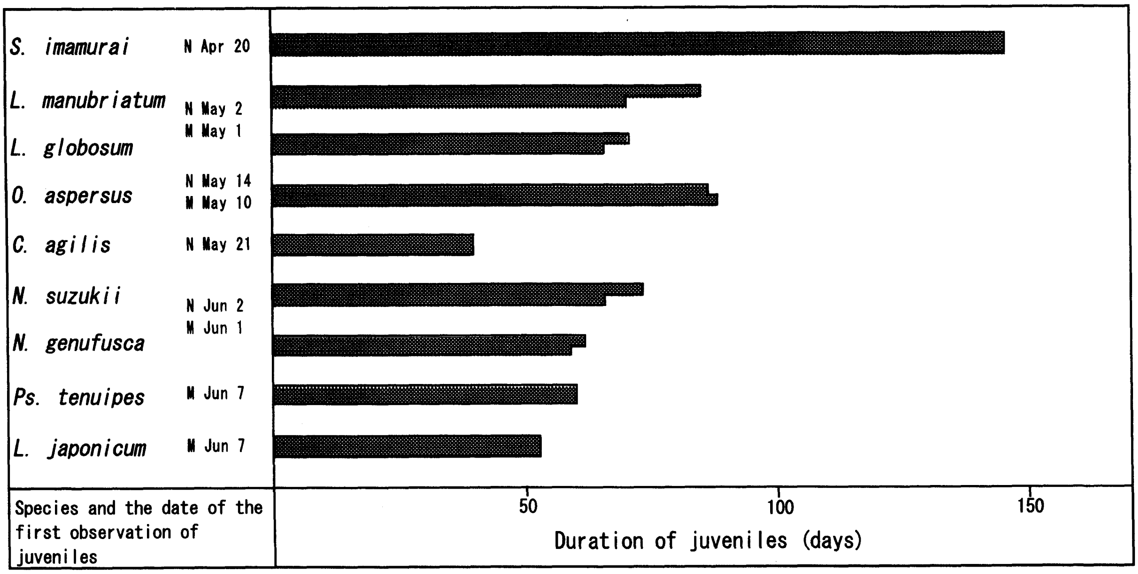


Fig. 9. Relationship between the length of juvenile period (days) and the order of the first emergence of juveniles. The date of the first observation in two *Leiobunum* (*manubriatum* and *globosum*) and two *Nelima* species (*genufusca* and *suzukii*) were combined because the identification was impossible at younger juvenile stages. When juveniles were collected in both Maruyama and Nopporo, the upper and the lower bars represent the length of juvenile periods in Nopporo and Maruyama, respectively.

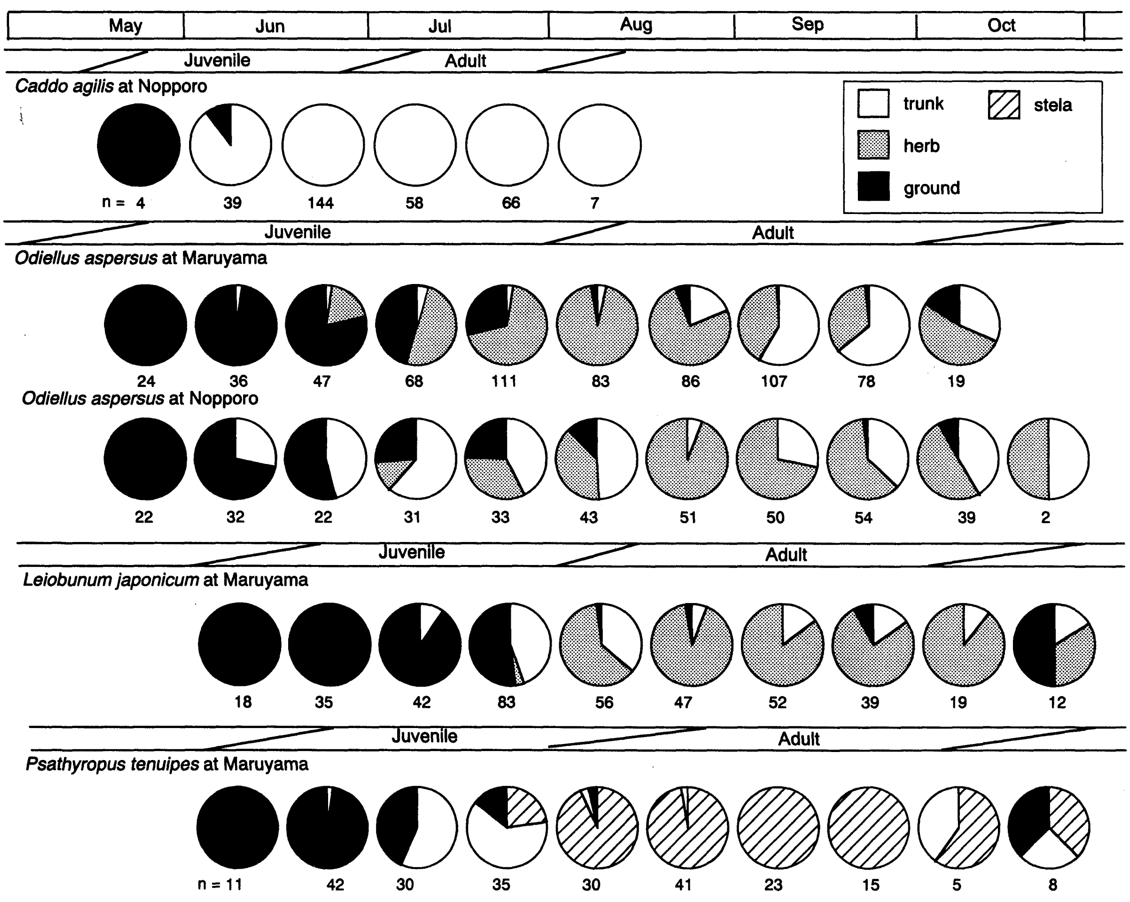


Fig. 10. Seasonal transition of microhabitat preference in *Caddo agilis, Odiellus aspersus, Leiobunum japonicum* and *Psathyropus tenuipes* in Maruyama and Nopporo. Each pie chart shows frequency distribution of individuals found on the ground, on herbs and on trunks of trees, respectively, based on the collection data bimonthly pooled.

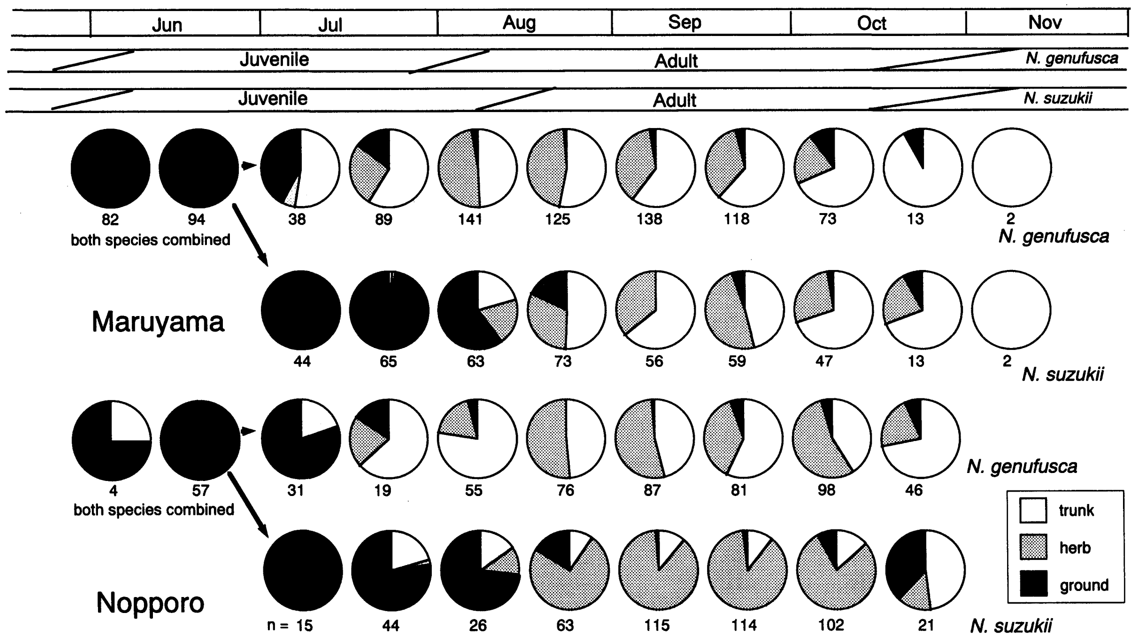


Fig. 11. Seasonal transitions of microhabitat preference in *Nelima genufusca* and *N. suzukii* n. sp. in Maruyama and Nopporo. Explanation as in Fig. 10.

earlier stages. They soon moved up to the lower part (less than 1 m in height) of tree trunks and stayed there until disappearance in mid August (Fig. 10). *Psathyropus tenuipes* also did not utilize herbaceous layer after they left from soil litter. Instead of herbs or tree trunks, adults of *Psathyropus tenuipes* showed special preference to inscriptions or other depressions on stone monuments as hiding places in the daytime.

For other species, preference for herbaceous layers decreased in the following order: *Leiobunum japonicum* > *Odiellus aspersus* > *Leiobunum globosum* + *L. manubriatum* > *Nelima suzukii* > *N. genufusca* (See Tsurusaki 1986 for *Leiobunum globosum* and *L. manubriatum*). Microhabitat preference at adult stage in *Nelima suzukii* was different from that in *N. genufusca* in Nopporo, though this trend was not demonstrated in Maruyama.

4. Sex ratio

A total of 6,918 individuals of harvestmen were collected in the three areas through the periodical surveys in 1979. Table 3 shows the number of individuals collected and sex ratio of each species given by male percentage in adults.

Significant deviations from the sex ratio 1:1 ($P<0.05$ in X^2-test) were observed in threee species in Maruyama and Nopporo. In three species, *Caddo agilis*, *Leiobunum manubriatum*, and *L. globosum*, males were very rare or never collected. These facts indicate that the populations of these species are maintained by parthenogenesis. Thelytoky of the two *Leiobunum* species and morphology of the rare males of *Caddo agilis* found in the present survey in Nopporo were already reported elsewhere (Tsurusaki 1986 and Suzuki & Tsurusaki 1983, respectively).

On the other hand, the dominance of male in number was observed in the following three species; *Odiellus aspersus* (67.3% in Nopporo, 64.2% in Maruyama), *Psathyropus tenuipes* (60.0% in Maruyama), *Leiobunum japonicum* (57.1% in Maruyama). The same trend was observed also in the Nopporo population of *Nelima genufusca*, while sex ratio in the Maruyama population was normal (47.8%).

5. Copulation and reproductive schedule with reference to the two species of *Nelima*

Figure 12 represents all the records of copulations observed in the field during the periodical survey and a preliminary survey arbitrarily conducted in 1978. Copulations were observed in only four species, *Odiellus aspersus*, *Leiobunum japonicum*, *Nelima genufusca*, and *N. suzukii*, and the observations were generally infrequent except for *N. genufusca*.

In *N. genufusca*, the first copulation was observed in mid August, about two weeks later than the first emergence of adult female, and the copulation was continuously observed until near the end of adult season. In *N. suzukii*, the copulations were more infrequently observed and limited to the last half of the adult period.

A case of interspecific copulation and a rush for courtship by a male to a heterospecific female were observed between the two species of *Nelima* at Maruyama in 1978. Both the cases occurred in a combination between male *N. genufusca* and female *N. suzukii*.

Table 3. Number of individuals and sex ratio of eleven species collected through the periodical survey at Maruyama (M), Nopporo (N), and the Campus of Hokkaido University (UC) in 1979.

Species	Loc.	Number of individuals collected[1)] juv.	adult male	adult female	adult ♂+♀	Sex ratio (%♂♂)[2)]
C. agilis	N	151	2	123	125	1.6**
O. aspersus	M	317	221	123	344	64.2**
	N	177	136	66	202	67.3**
L. japonicum	M	163	128	96	224	57.1*
L. manubriatum	M	86	0	221	221	0.0**
	N	5	0	10	10	0.0**
L. globosum	M	3	0	28	28	0.0**
	N	152	23	455	478	4.8**
N. genufusca	M	142	287	313	600	47.8
	N	70	236	173	409	57.7**
N. suzukii	M	166	118	138	256	46.1
	N	92	206	199	405	50.9
Ps. tenuipes	M	134	63	42	105	60.0*
S. makinoi	M	53	8	12	20	40.0
	N	120	38	52	90	42.2
S. imamurai	M	25	0	0	0	–
	N	37	27	31	58	46.6
Pa. pumilio	UC	463	285	256	541	52.7

[1)] The following specimens obtained by some additional collectings on particular species in the same year are excluded: *Leiobunum manubriatum* (19 juveniles and 49 females) and *L. globosum* (5 females) from Maruyama; *Caddo agilis* (15 juveniles and 27 females), *L. manubriatum* (2 juveniles, 1 female) and *L. globosum* (44 juveniles, 11 males, 166 females) from Nopporo.

[2)] $*p<0.05$, $**p<0.01$ in χ^2 test (significant deviation from the ratio 1:1)

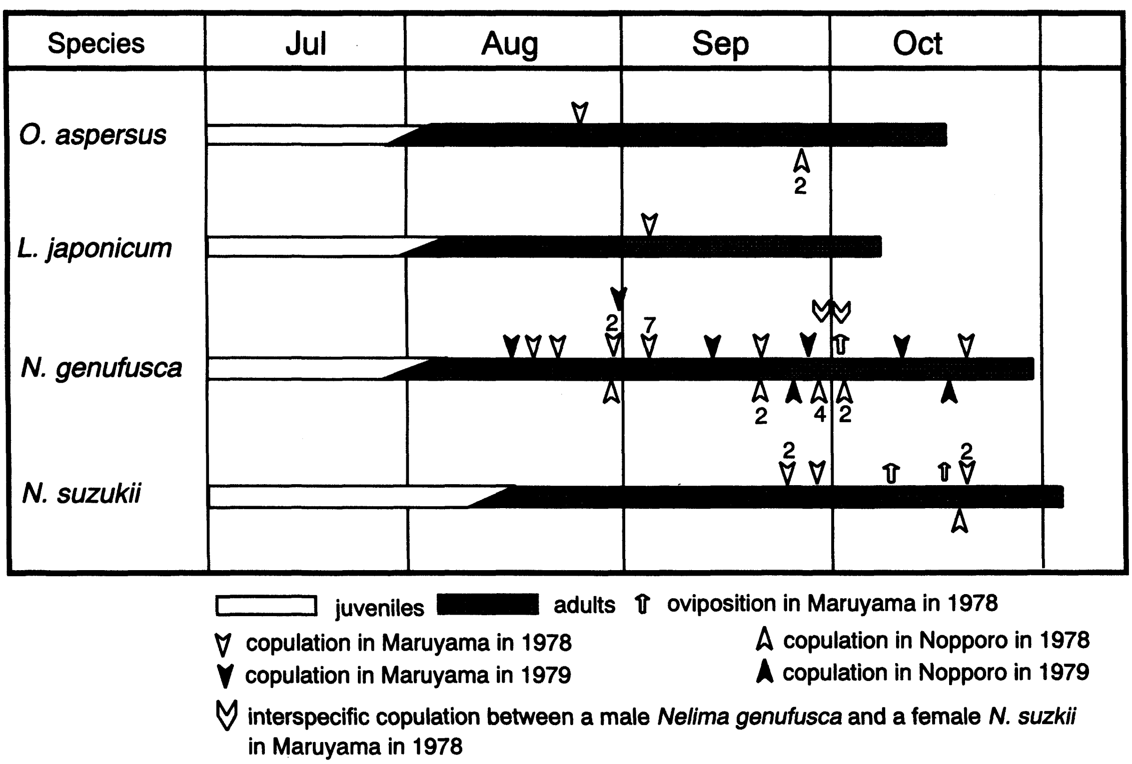


Fig. 12. Seasonal distribution of the records of copulation and oviposition in four harvestman species in 1978 and 1979 in Maruyama and Nopporo. The number of copulations observed in the same day are shown by numerals beside arrows.

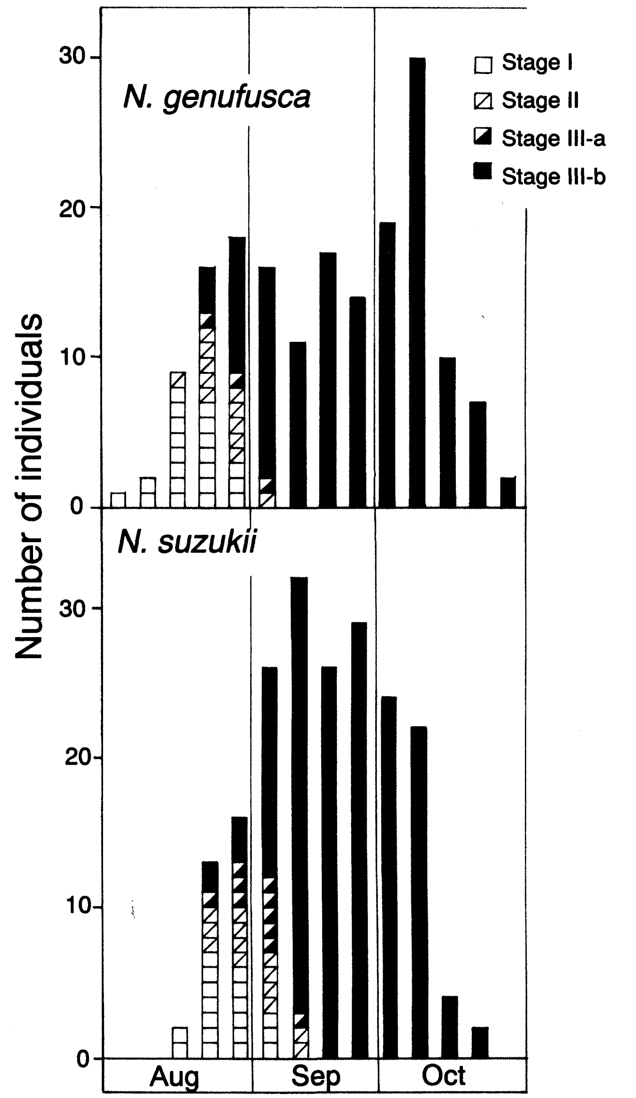


Fig. 13. Seasonal changes of ovarian development in *Nelima genufusca* and *N. suzukii* n. sp. in Nopporo in 1979. Each box represents one female. Ovarian conditions were classified into four stages: Stage I (immature ovary) — oocytes without any indication of yolk accumulation; Stage II — yolks are accumulated in oocytes but mature eggs are not formed yet; Stage IIIa — mature eggs are retained in ovary, not in the egg reservoir (uterus internus); Stage IIIb — mature eggs are retained in both ovary and the egg reservoir.

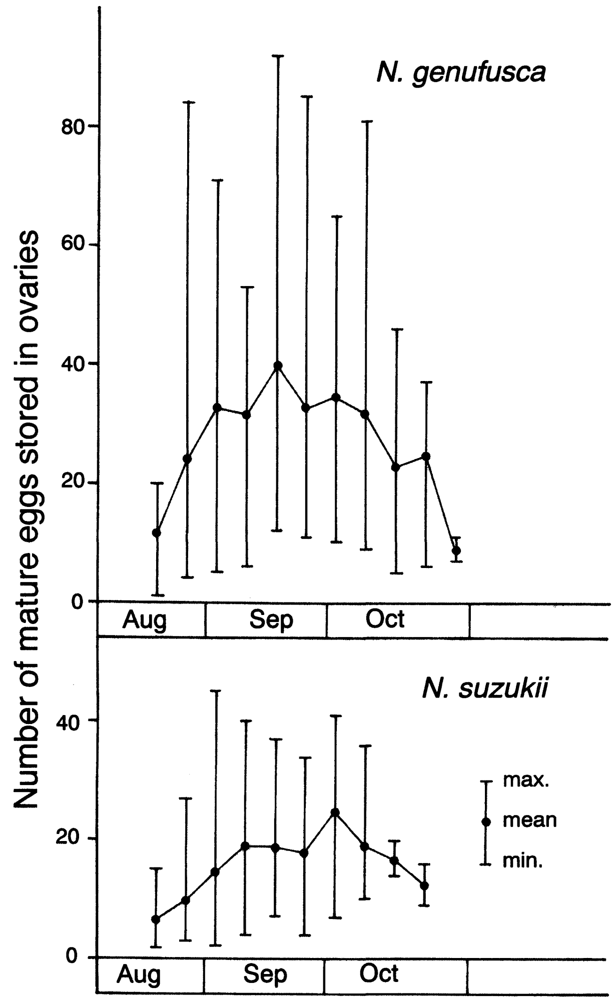


Fig. 14. Seasonal changes of numbers of mature eggs retained by females (stage III) of *Nelima genufusca* and *N. suzukii* collected in 1979.

Ovarian development in the two species of *Nelima* is shown in Fig. 13. Ovaries of *N. suzukii* developed about a week later than those of *N. genufusca*. The number of matured eggs stored in ovaries of *N. genufusca* (means in the peak reproductive period ranged from 32 to 40) was about twice larger than that of *N. suzukii* (means around 18–22, Fig. 14).

6. Number and size of eggs

Egg sacs of two species of *Sabacon* were sporadically found in damp places under stones or logs in the field (Fig. 7). Each egg sac was dome-shaped and consisted of several eggs and transparent mucous jelly that enveloped eggs (Fig. 15A). The mucous jelly severely shrunk when the egg sac was kept in dry container for only a couple of hours, while it easily absorbed water and restored its shape when it was misted by an atomizer. It seems that the mucous jelly has a function to prevent desiccation of eggs in addition to the other functions to protect eggs from fungus attack or predation by other invertebrates. This type of mucous egg sac has been reported only in *Ischyropsalis* (Ischyropsalididae of the Superfamily Ischyropsalidoidea to which Sabaconidae also belongs) and *Mitostoma* (Nemastomatidae of the Superfamily Troguloidea) (Juberthie 1964, 1965). In *Sabacon makinoi* average size of the egg sacs is 2.18 mm (range: 1.89–2.39, n=9) in diameter and 3.07 mm (2.27–3.65, n=9) high. Egg sacs of *Sabacon makinoi* were found from late July to early November in the field and in late June (24 June 1979) in captivity, though they were most frequently found in the field in fall (Fig. 7). The number of eggs per egg sac varied from 6 to 20 with a

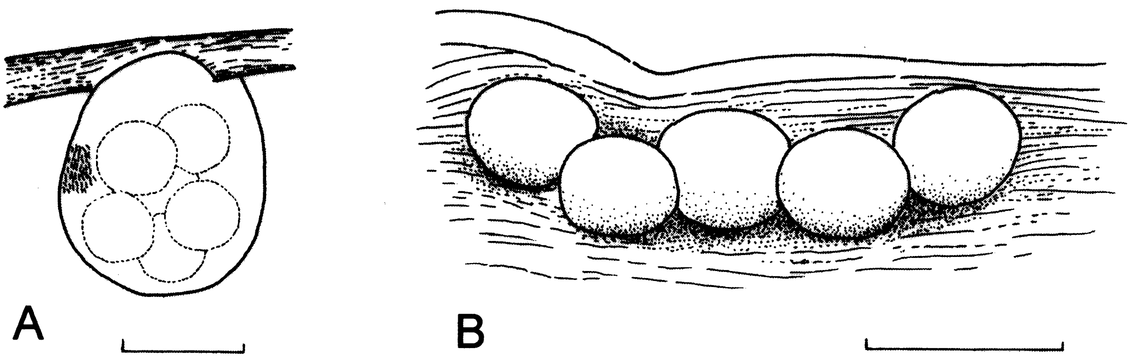


Fig. 15. Eggs of *Sabacon imamurai* and *Paraumbogrella pumilio*. A: An egg sac of *Sabacon imamurai* found beneath a fallen log on the ground in Nopporo on 14 May 1979. The egg sac was mucous and attached to a fibrous root. Six eggs were visible through the transparent mucous jelly, although whole surface of the jelly was finely wrinkled as partly illustrated. B: Eggs of *Paraumbogrella pumilio* laid on 9 June 1979 under laboratory conditions. In this case, nine eggs, of which 5 eggs are shown here, were laid at once as a cluster inside a piece of straw. Scales = 1 mm.

Table 4. Number of eggs laid by female *Paraumbogrella pumilio* reared in the laboratory from 7 May to 13 August in 1979.

Number of egg cluster[1)]	Code number for female							
	#1	#2	#3	#4	#5	#6	#7	#8
1st	6	3*	6	6	9	9*	9	9
2nd	3	–	–	6	2	1	6	5
3rd	8*	–	–	6	4	5*	3*	5
4th	5*	–	–	2*	4	–	3	8
5th	–	–	–	1*	4	–	–	–
Total number of eggs	22	3	6	21	23	15	21	27
First observed[2)]	5/23	6/16	5/31	5/15	5/26	6/9	5/27	5/12
Last observed[2)]	6/24	6/16	5/31	7/17	6/10	6/25	6/28	5/30
Death of the female[3)]	–	6/16	7/14	7/22	7/5	7/19	–	–

[1)] Clusters of eggs are arranged according to the order of the discovery. Some clusters consisting of developing eggs show the egg clusters were laid several days prior to the date of the discovery. This means the order does not represent the actual order of oviposition. Clusters with developing eggs are shown with asterisks.

mean 11.4±3.8 (n=23: of these 21 were found in the field and 2 were obtained in laboratory raring). Further, four egg sacs only with one or two undeveloped eggs were found in 25 September and 2 October in Nopporo. They were considerd as egg sacs from which juveniles hatched had already left. The number of egg sacs produced by a female of *S. makinoi* is unclear, though a female collected from Maruyama on 20 June 1978 and kept in the laboratory laid two egg sacs by 24 June. In the case of *Sabacon imamurai* only two egg sacs both containing 6 eggs were found on 14 May 1979 at Nopporo (Fig. 15A).

Eggs of all the species except for the two species of *Sabacon* are devoid of special medium that protects eggs, and are laid directly in clusters in the crevices, soil litter, dead plant materials on the ground (Fig. 15B). Such kind of eggs were not found in the field. Information on the number of eggs was available only from some females reared in the laboratory. Data on the number of eggs obtained from eight females of *Paraumbogrella pumilio* are presented in Table 4. Condition of two females (#2 and #3) were considered to be far from normal due to extremely small number of eggs (3 and 6). Excluding these females the average number (±SD) of eggs was 21.5±3.9 (n=6).

Comparable data on other species of Phalangioidea are fewer. The total numbers of eggs per female obtained from three of five females kept in laboratory of *Nelima genufusca* were respectively 86 (2 batches: 15 and 71), 58, and 46 (Since no eggs were obtained in two females, the average number of eggs per female is 63). Of five females of *Nelima suzukii* reared, only one female laid eggs and the number of eggs was 18 (two batches: 8 and 10). In *Odiellus aspersus* and *Psathyropus tenuipes,* 79 and 143 eggs, respectively, were laid by one female each.

Table 5 summarizes egg size of 10 species. Eggs were approximately spherical (major axis / minor axis=ca. 1.1) in most species, though only that of *Sabacon imamurai* was oval-ball-shaped (major axis / minor axis = ca. 1.44). Comparison of egg sizes between before and after oviposition in 6 species showed eggs laid were 1.03-1.13 times (1.09 times on average) larger than the mature eggs

Table 5. Egg size of ten species of harvestmen. Measurements (in mm) were carried out for eggs laid or mature eggs in egg reservoir in adult females.

Species[1)]	Locality[2)]	n	Length of major axis		Length of minor axis	
			mean±SD	range	mean±SD	range
Odiellus aspersus	Maruyama	30	0.97±0.02	0.91–1.00	0.94±0.03	0.88–0.99
*Odiellus aspersus**	Maruyama	48	0.93±0.04	0.80–1.03	0.83±0.03	0.76–0.89
*Leiobunum japonicum**	Maruyama	40	0.61±0.03	0.56–0.67	0.51±0.02	0.48–0.53
Leiobunum manubriatum	Maruyama	39	0.87±0.06	0.78–1.08	0.78±0.06	0.65–0.88
*Leiobunum manubriatum**	Maruyama	6	0.79±0.03	0.76–0.83	0.66±0.03	0.61–0.69
Leiobunum globosum	Nopporo	83	0.94±0.06	0.83–1.13	0.83±0.04	0.70–0.95
Leiobunum globosum *	Nopporo	6	0.84±0.07	0.77–0.95	0.69±0.01	0.68–0.71
Nelima genufusca	Maruyama	30	1.12±0.07	1.01–1.28	1.03±0.04	0.94–1.08
*Nelima genufusca**	Maruyama	30	0.99±0.03	0.92–1.05	0.88±0.02	0.81–0.94
Nelima suzukii	Maruyama	50	0.92±0.06	0.81–1.00	0.83±0.09	0.60–0.95
*Nelima suzukii**	Maruyama	86	0.89±0.04	0.78–0.98	0.75±0.02	0.67–0.80
Psathyropus tenuipes	Botanical Garden	30	0.89±0.02	0.83–0.94	0.86±0.02	0.80–0.89
*Psathyropus tenuipes**	Botanical Garden	76	0.81±0.03	0.70–0.88	0.69±0.03	0.61–0.75
Paraumbogrella pumilio	University Campus	46	0.68±0.04	0.60–0.84	0.60±0.04	0.50–0.68
Sabacon makinoi	Maruyama & Nopporo	8	0.51±0.01	0.50–0.53	0.47±0.02	0.45–0.50
Sabacon imamurai	Nopporo	2	0.58	0.56–0.59	0.51	0.48–0.54

[1)] Asterisked: Measurements of mature eggs in egg reservoir (uterus internus) in adult females.
[2)] Botanical Garden: The Botanical Garden of Hokkaido University in Sapporo

preserved in egg reservoir of female reproductive organ (Fig. 16). Mean egg size ranged from 0.51×0.47 mm in *Sabacon makinoi* to 1.12×1.03 mm in *Nelima genufusca*. There was a linear correlation between body length of females and egg size (Fig. 16).

Discussion

1. Hibernating stages in Japanese Palpatores

The seasonal life cycle trends of the eleven species surveyed are schematically summarized in Fig. 17. Following three types of life cycle were recognized on hibernating stage:

1) Hibernation as eggs (9 species): All the species except for *Paraumbogrella pumilio* and *Sabacon makinoi* have this type of hibernation. These species showed more or less similar life cycle trend, being univoltine with maturation in summer.

2) Hibernation as adults (1 species): *Paraumbogrella pumilio* overwinters in the adult stage. Juveniles, which emerged in mid June, become adults from early October. Some post hibernating adults which can be distinguished from the newly recruited adults by degrees of melanism or injury of body survived until mid September. Copulation and oviposition take place in spring.

3) Hibernation as both eggs and juveniles (1 species): life cycle of *Sabacon makinoi* is not yet fully known, because the number of specimens collected through the periodical surveys was rather poor. Both adults and juveniles of several stages were collected almost throughout the surveys. Therefore this species seems to have no fixed life cycle and overwinter as various stages of juveniles and eggs.

The hibernation types exhibited by opilionid species in and near Sapporo are compared with those of Mt. Saragamine near Matsuyama, Shikoku, southern Japan (Tsurusaki, unpublished data based upon year-round occasional collections during 1971–1977). Table 6 shows the hibernation types of the species of suborder Palpatores from the two areas. Some species belonging to suborder Laniatores have also been recorded from Hokkaido (1 species: *Kainonychus akamai esoensis*) and Mt. Saragamine (3 species: *Pseudobiantes japonicus, Iyonus yuyama*, and *Nipponychus japonicus*). However, they are not treated here because life cycles of these species of Laniatores seem to be perennial, though they are not yet fully known.

In addition to the three types of life cycle presented above, the assemblage of palpatorid species in Mt. Saragamine has another type of life cycle, hibernation at juvenile stages. This type of hibernation is known in three species (*Opilio spinulatus, Leiobunum japanense*, and *Gagrellopsis nodulifera*) and make up 17.6% of all Palpatorid species in this area. These species have more or less similar life cycles with hibernating as juveniles of mid or later instars and molting to adult in spring. Lack of this type of hibernation in Hokkaido and the distribution of the three species with juvenile hibernation in southern Japan strongly suggest the relationship between juvenile hibernation and warm climate, although only *G. nodulifera* reaches Yamagata Prefecture, northern part of Honshu. Comparison of the species number among four types of hibernation shows that hibernation in egg stages is exceedingly dominant (84.6%) in Hokkaido, while 68.4% in Saragamine. Thus, in Palpatores, there seems to be a tendency that hibernation in egg stage is more prevalent in northward.

Four species (*Caddo agilis, Odiellus aspersus, Leiobunum japonicum, Psathyropus tenuipes*) are common to both areas, but no clear difference in life cycle of these

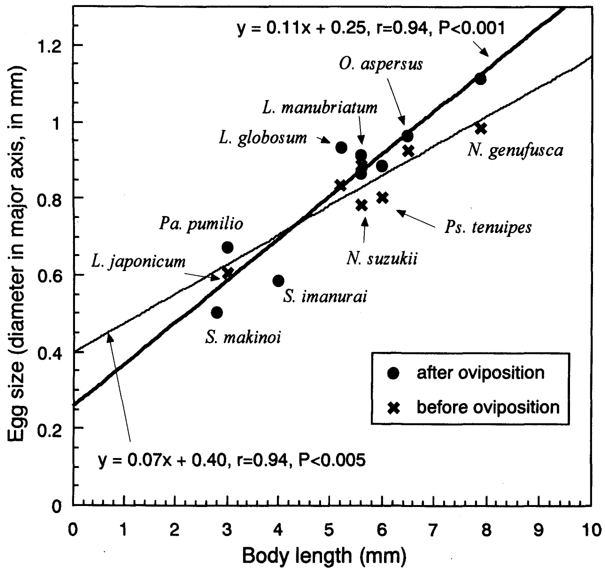


Fig. 16. Relationship between the egg size and female body length in 10 species of harvestmen. Note that eggs laid were always slightly larger than mature eggs stored in female body before oviposition.

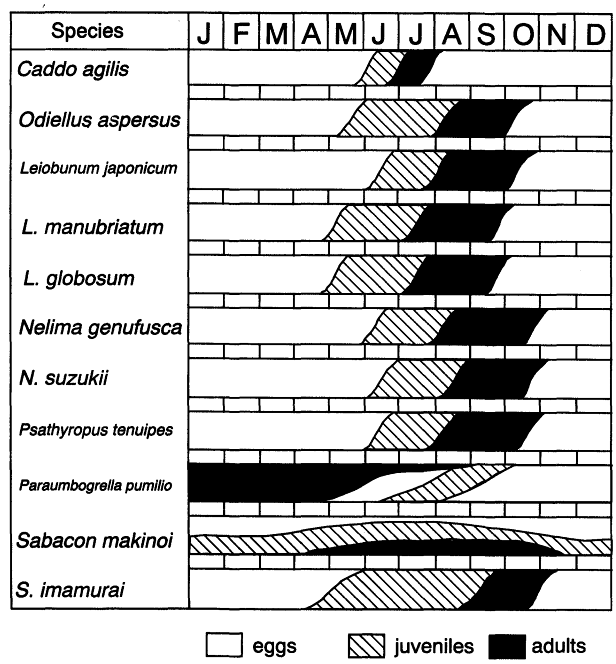


Fig. 17. Diagram of the life cycles of 11 opilionid species in and near Sapporo.

species was observed; all these species are univoltine in both Hokkaido and Shikoku. Southward increase in the number of generations has not been documented in any species of harvestmen, as far as I know, except for a single species, *Phalangium opilio* (Newton & Yeargan 2002).

Next, the relationship between life cycle and phylogeny is mentioned based upon the hibernation stages of the species in Table 6, because those species cover almost all the genera of suborder Palpatores known from main islands of Japan. As illustrated in Fig. 18, the type of hibernation is rather uniform within a family or a genus, though there are some exceptions. For example, species of the genus *Leiobunum* usually hibernate as eggs but only one species, *Leiobunum japanense*, hibernates as juveniles. Variation in life cycle may occur even at the level of genus. Life cycle of species of the genus *Sabacon* is of much interest from such aspect. Phenology of two species of the *pygmaeus* group (*S. pygmaues* and *S. makinoi*) is distinctly different from that of 2 species of the *dentipalpus* group (*S. satoikioi* and *S. imamurai*).

It must be emphasized that two species of subfamily Gagrellinae of the family Sclerosomatidae (*Systenocentrus japonicus* and *Paraumbogrella pumilio*) with adult overwintering have small body and relatively short legs and inhabit the litter on the ground throughout their lives as well as all the species of superfamilies Ischyropsalidoidea and Troguloidea.

2. Relationship between hatching date and length of juvenile period

The seven species with egg overwintering showed an interesting tendency that the earlier they emerge in spring, the slower they grow (Fig. 9). Low metabolic rate, low foraging activity probably associated with low temperature in earlier season just after the thawing, and possible paucity of small invertebrates available for food for young harvestmen might partly explain the trend. However, why there is so much temporal variation in emergence time of juvenile among species is unclear.

It is also interesting that adults of three parthenogenetic species, *Caddo agilis, Leiobunum manubriatum* and *L. globosum* emerge earlier than other species. Earlier starts of both juvenile and adult stages might be advantageous for reducing competition for resource with other sexual species of harvestmen. However, it has been thought that competition over food is usually unlikely to occur because their potential diets are considered to be abundant (Adams 1984). Thus, no persuasive explanation for the unique life cycles of the three parthenogenetic species is available at present.

3. Protogyny

Protogyny, which means female precedence over male for the maturity, is extremely rare among insects and other invertebrates (Thornhill & Allcock 1983). However, this trend has been noted at least in two species of harvestmen: *Mitopus morio* (Phalangiidae: Oligolophinae) in Norway (Slagsvold 1976) and *Dicranopalpus ramosus* (Sclerosomatidae, Gyinae or family *incertae sedis*: *Dicranopalpus*-species group: Crawford 1992) in Spain (Rambla 1986). Earlier peak of female activity has been reported also in *Odiellus triangularis* (Phalangiidae: Oligolophinae) in Spain (Rambla 1986) and *Nemastoma lugubre* (Nemastomatidae) in the Netherlands (Meijer 1972), though

Table 6. Comparison of hibernating stages between 15 species of the suborder Palpatores in Hokkaido and 19 ones in Shikoku (Mt. Saragamine)

Stage of hibernation	Sapporo 43°N (Hokkaido) 15 species[1)]	Mt. Saragamine 33.5°N (Shikoku) 19 species[2)]
Egg	13 species (86.6%)	13 species (68.4%)
	Caddo agilis	*Caddo agilis*
	Odiellus aspersus	*Odiellus aspersus*
	*Mitopus morio**	*Leiobunum japonicum*
	*Phalangium opilio**	*L. montanum*
	*Homolophus arcticus**	*Nelima nigricoxa*
	Leiobunum japonicum	*N. satoi*
	L. manubriatum	*N. parva*
	L. globosum	*Psathyropus tenuipes***
	Nelima genufusca	*Gagrelllula ferruginea*
	N. suzukii	*G.* sp.
	Psathyropus tenuipes	*Melanopa grandis*
	Sabacon imamurai	*Sabacon satoikioi*
	*Nipponopsalis yezoensis**	*Nipponopsalis abei*
Juvenile		3 species (15.8 %)
		*Opilio spinulatus***
		Leiobunum japanense
		Gagrellopsis nodulifera
Adult	1 species (6.7 %)	2 species (10.5 %)
	Paraumbogrella pumilio	*Systenocentrus japonicus*
		Dendrolasma parvulum
Egg and juvenile	1 species (6.7%)	1 species (5.3%)
	Sabacon makinoi	*Sabacon pygmaeus*[3)]

1) *Assumed from occasional collection data.
2) Tsurusaki unpublished. **Species collected from Matsuyama city at the foot of Mt. Saragamine
3) Amended here from *Sabacon pygmaeum* Miyosi 1942 since the gender of the genus name *Sabacon* was found to be not neuter but masculine (Gruber 2003)

protogyny has not yet been detected in those species.

The present study revealed that females reach adulthood about a week earlier than males in as many as eight species out of nine species with an annual cycle with egg hibernation and hatching in spring. It is difficult to detect protogyny unless intervals between the two consecutive surveys are about one week or less. Therefore it is likely that protogyny is more widespread in harvestmen of the superfamily Phalangioidea.

Why do males show retarded maturation in those harvestmen? Some of the properties in reproductive ecology of harvestmen may explain the phenomenon. First, at least several days are required for ovarian maturation after adult eclosion in females (cf. Fig. 13). Possibly in connection with this term for ovarian maturation, females do not become receptive for copulation for at least about a week after their final molt. Second, females mate frequently for a relatively long reproductive season, at least one month (Edgar 1971; Macías-Ordóñez 1997). In those females that mate multiple times, it is likely that the sperm ejaculated by the last male could be preferentially used for insemination. In such situation, it is possible that the males which reach adulthood earlier than other males cannot leave more offspring. Further, staying longer as juveniles may be advantageous for males if it leads to larger body size and larger body is favorable in male-male competition for copulation with females. It has revealed that larger males of *Nelima nigricoxa* tend to make more nestling pairs consisting of a female and a male, which are considered to be postcopulatory mate guarding, than smaller ones (Okada and Tsurusaki, unpubl.). Therefore, growing larger than other males may be important as a male mating strategy.

Female precedence in adult emergence was not found in *Psathyropus tenuipes*. This species seems to have rather versatile life history and there is a wide range of temporal variation in both hatching and adult eclosion. Due to this, juveniles are found with adults for a long period extending to about 3 weeks in the Maruyama population. In southwestern Japan, the duration of the coexistence in *Psathyropus tenuipes* extends to as much as more than 2 months (Tsurusaki 1993 and unpublished data). Thus, protogyny would not evolve in species with asynchronous adult eclosion.

In this context, absence of protogeny in *Paraumbogrella pumilio* is also understandable. There is a long period of reproductive dormancy between the final molting to adulthood in fall and the onset of reproduction in the next spring in this species. In such situation, differential adult

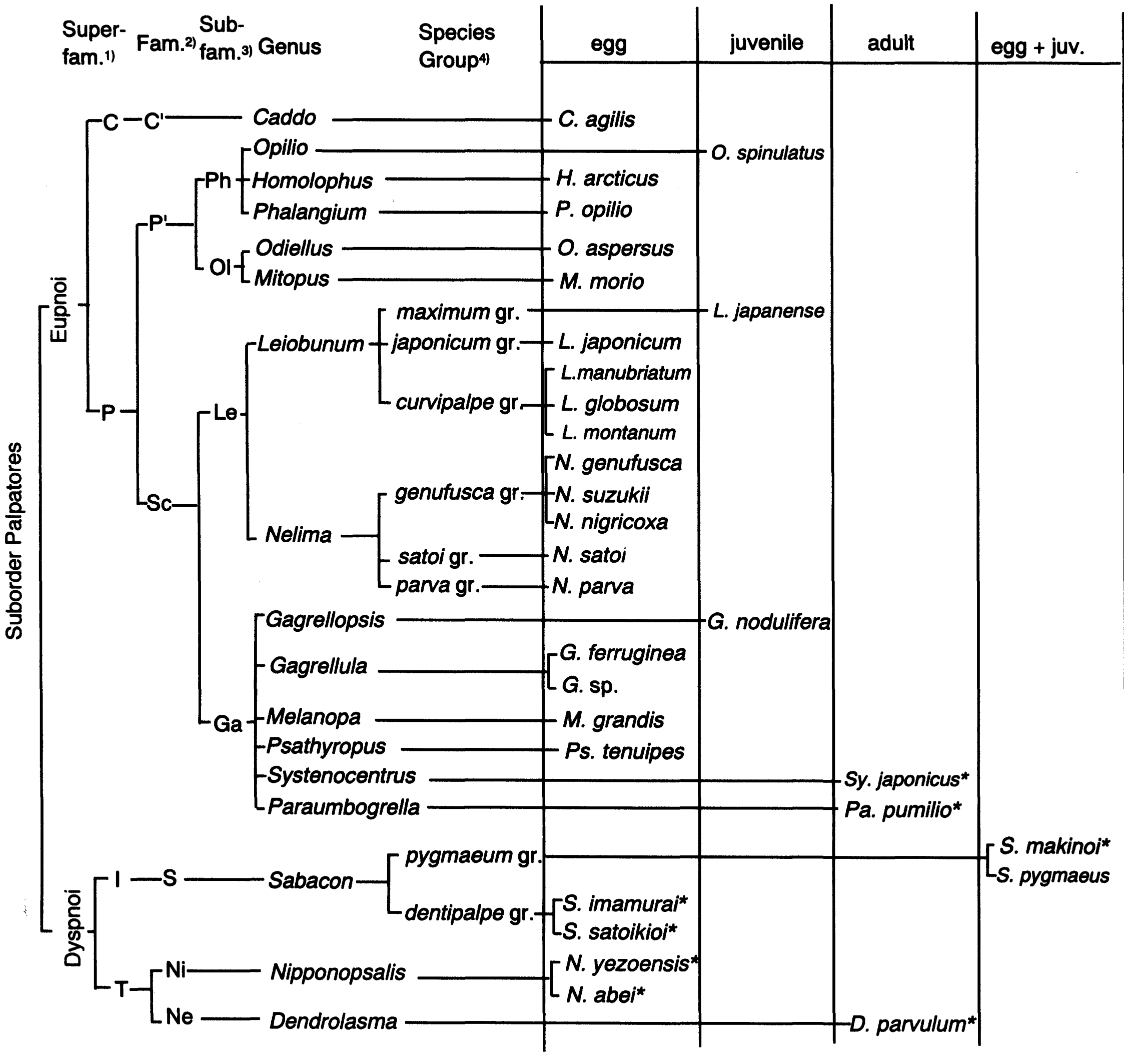


Fig. 18. Major classification of Palpatores species presented in Table 6 and their hibernating stage. Major classification system follows Martens (1978), although adoption of a dichotomy for Dyspnoi/Eupnoi follows Giribet et al. (1999, 2002) and Shultz & Regier (2001) and family names within Phalangioidea follow Crawford (1992). 1-3) Scientific names abbreviated with initial letters: 1) Superfamily: C = Caddoidea, P = Phalangioidea, I = Ischyropsalidoidea, T = Troguloidea, 2) Family: C′ = Caddidae, P′ = Phalangiidae, Sc = Sclerosomatidae; S = Sabaconidae, Ni = Nipponopsalididae, Ne = Nemastomatidae. 3) Subfamily: Ph = Phalangiinae, Ol = Oligolophinae, Le = Leiobuninae, Ga = Gagrellinae). 4) Species groups follow Suzuki (1976) for *Leiobunum*, Suzuki (1974 b) for *Nelima*, and Suzuki (1974 a) for *Sabacon*.

emergence between the sexes over one or two weeks would not affect the reproductive success of males.

However, to make this explanation for evolution of protogyny in harvestmen more persuasive, the following points have to be ascertained in further study. First of all, sperm precedence pattern, of which no data has so far been available in harvestmen, should be clarified in these harvestmen. Further, we need information on the length (days) from the final molt of males to the onset of copulation with females.

4. Sex ratio

It has been often reported that overall sex ratio of adult harvestmen in the field often deviates from normal 1:1 even in bisexual species (Pfeifer 1956; Macías-Ordóñez 1997). Pfeifer (1956) reported that males of *Nemastoma lugubre* (Nemastomatidae) and *Lacinius horridus* (Phalangiidae: Oligolophinae) were always more frequently observed than females in the field, whereas females predominated over males in other species. In the present study, male-biased sex ratio was observed in three (*Odiellus aspersus, Leiobunum japonicum*, and *Psathyropus tenuipes*) of the five long-legged species and in the Nopporo population of *Nelima genufusca* (Table 3). The trend was generally persistent over adult period after the adult male emergence. In those male-biased species, however, sex ratios show

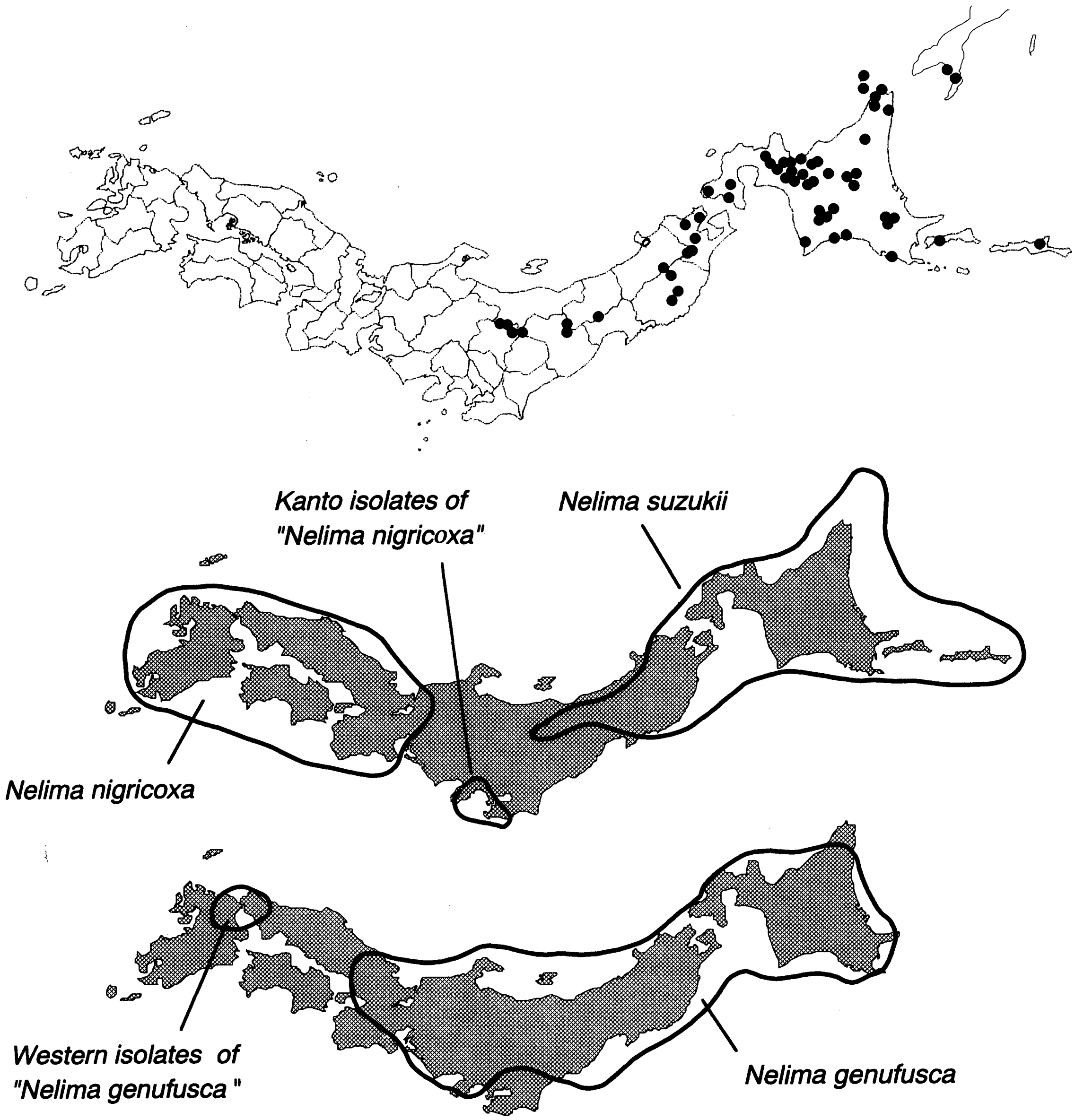


Fig. 19. Distribution of *Nelima suzukii* n. sp. (top) and outlines of the distributional ranges of other species of the *genufusca*-group of *Nelima* (middle and bottom). *Nelima nigricoxa* has Kanto isolates in Izu Peninsula, the Hakone area, Miura and Bosô Peninsulas (middle), while *N. genufusca* has western isolates in northern Kyushu and western part of Yamaguchi Prefecture of Honshu (bottom). *Nelima genufusca* is sympatric with *N. nigricoxa* in (1) northern Kyushu and western part of Yamaguchi Prefecture of Honshu, (2) northern part of Kinki District, (3) Izu Peninsula and the Hakone area. *N. genufusca* is sympatric also with *N. suzukii* n. sp. in northern Honshu and most of Hokkaido. *N. suzukii* is also distributed in Sakhalin, Is. Rebun, Is. Rishiri, Is. Kunashir, and Is. Iturup.

approximately 1:1 when they were determined in penultimate juveniles. Therefore, these male-biased sex ratios are attributable to the difference in microhabitat preference between the sexes. Unfortunately, no statistically significant differences in microhabitat preference were detected between the sexes in this study. It is likely that females prefer concealed places within the undergrowth of shrubs, herb, or *Sasa* bamboos so as to lay eggs in the humid crevices of the ground in the later stages of adult period. If these male-biased sex ratios in later reproductive season are caused by non-participation of gravid females, they represent male-biased operational sex ratio (OSR). Male-biased OSR can facilitate postcopulatory mate guarding (Yamamura 1986). Postcopulatory mate guarding is often exhibited by males of the two species of *Nelima* in late reproductive season. Actually, we have recently found that there is a strong correlation between frequency of postcopulatory mate guarding and sex ratios in *Nelima nigricoxa*, which is distributed in

western Japan (Okada and Tsurusaki, unpubl.). Thus, it is very likely that the male-biased sex ratios bring about important effects in mating tactics of males and sexual selection in these harvestmen. Further study with mark-recapture method is needed to ascertain accurate cause of the male-biased sex ratio and relevance of the male-biased sex ratio to the postcopulatory mate guarding.

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Appendix: Taxonomical notes on two species of *Nelima* found in Hokkaido

The larger and the smaller species of the genus *Nelima* (Sclerosomatidae: Leiobuninae) sympatrically distributed in Hokkaido were recorded respectively as *Nelima gigantea* (Loman 1902) and *N. genufusca genufusca* (Karsch 1881) in Suzuki & Tsurusaki (1983). However, Suzuki found later that the type specimen of "*N. genufusca genufusca*" is conspecific with the larger species which was called "*Nelima gigantea*" in Suzuki & Tsurusaki (1983) and proposed that "*Nelima gigantea*" should be replaced by the older name "*N. genufusca genufusca*" (Suzuki 1985). Although he alluded that the smaller species belongs to *N. nigricoxa* Sato & Suzuki 1939 or its allies, no conclusion was presented there, and hence the smaller species has been in a nameless situation. I consider the smaller species which is widely sympatric with the larger species "*N. genufusca*" in Hokkaido is not *Nelima nigricoxa* but a distinct new species as described below.

Nelima suzukii n. sp.
[Japanese name: Ezonami-zatômushi]
(Fig. 1F–G, 19)

Nelima genufusca: Suzuki 1941, p. 247.
Nelima genufusca: Suzuki 1949, p. 18.
Nelima genufusca genufusca: Suzuki & Tsurusaki 1983, p. 223, figs. 20 A-B, 22; Tsurusaki & Hayashi 1985, p. 509.
Nelima sp. B (Ezonami-zatomushi in Japanese): Tsurusaki 1985
Nelima sp. (Ezonami-zatomushi): Tsurusaki & Ôhara 1997, p. 33.

Type series. Holotype: male from Nopporo, Ebetsu-shi, Hokkaido, Japan, 20-IX-1979, collected by N. Tsurusaki. Paratypes: 5 males and 7 females collected at the type locality in 28-VIII-1978 by N. Tsurusaki. They are deposited in National Science Museum, Tokyo (NSMT).

Diagnosis and description. Detailed description and diagnostic characters of this species can be found in Suzuki & Tsurusaki (1983). The holotype designated here is the specimen on which illustrations (fig. 22 A, C-D, G, I-J, L-M) presented in the paper were made. Diagnostic characters between *N. suzukii* and *N. genufusca* are tabulated in table 3 in Suzuki & Tsurusaki (1983). Note that there is a typographical error in the table: read "♂ 6.1–7.7 mm, ♀6.1–7.7 mm" as "♂ 6.1–7.7 mm, ♀5.0–6.8 mm" in the length of femur I of *N. suzukii* (as "*genufusca*" in the table) and "♂ 8.4–12.2 mm, ♀ 8.5–10.8 m" as "♂ 8.4–12.2 mm, ♀8.5–10.8 mm" in length of femur I of *N. genufusca* (as "*gigantea*" in the table). In addition to the list, *N. suzukii* may be distinguished from *N. genufusca* by its glossy coloration on the dorsum especially in fully matured males.

Measurements. Mesurements based on the Nopporo population are also presented in Suzuki & Tsurusaki (1983). Only mesurements (in mm) of the male holotype is presented here: Body 3.8 long; cephalothorax 1.15 long, 2.4 wide; abdomen 2.65 long, 2.29 wide. Length of palp and legs (Fe / Pa / Ti / Mt / Ta = Total): palp, 0.80 / 0.63 / 0.70 / - / 1.44 = 3.57; leg I, 7.0 / 1.3 / 6.4 / 8.2 / 13.0 = 35.9; leg II, 11.4 / 1.4 / 11.1 / 12.1 / 31.0 = 67.0; leg III, 7.1 / 1.5 / 6.4 / 9.1 / 13.7 = 37.8; leg IV, 9.3 / 1.6 / 8.9 / 10.0 / 21.8 = 51.6.

Specimens examined. Specimens whose records can be found in Suzuki & Tsurusaki (1983) are not listed here. All the specimens are in my private collection at Tottori University. Data are given by the following order: locality, altitude of locality if available, number of individuals (juv. = juvenile), date collected, collected by (NT = N. Tsurusaki). SAKHALIN. Korsakov District: environs of Ozerskiy Village, Lake Bolshoye VaVaiskoye, 1 juv., 2-VIII-1985, A. M. Basarukin; south shore of Lake Tunaycha, 3♂1♀, 26-IX-1991, A. M. Basarukin. KURILS. Is. Itrup, Chirip Peninsula, 1♂1♀, 31-VIII-1995, Y. Marusik. Is. Kunashir, near Yuzhno-Kuril'sk: 2 juv. (1 juvnile female for chromosome observation), 2-VIII-1995, Y. Marusik; 1♂, 1-IX-1995, Y. Marusik. HOKKAIDO. Is. Rebun: Mt. Rebun, 100 m, herbaceous grassland, 1♀, 2-IX-1991, N. Yasuda and M. Sato; R. Kabukai, 30–50 m, 6 juv., 10-VIII-1990, Y. Nishikawa. Is. Rishiri, Himenuma: 130–180 m, 1♀2 juv., 7-VIII-1985, NT; Doba, 100 m, 2juv., 7-VIII-1990, Y. Nishikawa. Is. Rishiri, Mt. Rishiri: From Oshidomari to Mt. Pon, 30–320 m, 10juv., 8-VII-1984, NT; Oshidomari course, 100–600 m, 35♂25♀, 12-IX-1984; 0–200 m, 1juv., 8-VIII-1985, NT; 100–500 m, 1♂1♀, 31-VIII-1990, E. Nishitani and M. Sato; 100–500 m, 1♂5♀, 28-IX-1990, E. Nishitani and M. Sato; Kutsugata course, 150–430 m, 72♂24♀, 11-IX-1984, NT. Wakkanai-shi: W akkanai-kôen, 60–100 m, 2juv., 7-VII-1984, NT; from Wakkanai Forest Park to Hyakunen-Kinentô, 100–120 m, 6♂, 11-IX-1984, NT. Sarobetsu Marsh: 3♂17♀, 11-VIII-1991; 1♂12-IX-1991; Nishi-Toyotomi, 1♀, 10-VIII-1991, all by N. Yasuda. Teshio-gun, Toyotomi-cho, Toyotomi Spa, 40 m, 1 ♀, 12-VIII-1990, Y. Nishikawa. Esashi-gun, Hamatonbetsu-cho, Beniya-Gensei-kaen, 14-VIII-1990, 1♂9♀1 juv., Y. Nishikawa & S. Ueno. Kawakami-gun, Teshikaga-cho, Lake Kussharo, near R, Toikoi, *Abies sachalinensis* forest, 130 m, 2♂1♀, 23-IX-1996, NT. Lake Daisetsu, Mts. Daisetsu, 2♀, 20-VIII-1994, N. Yasuda. Asahikawa-shi, Kamuikotan, 4♂3♀, 17-VIII-1984, NT. Ebetsu-shi, Nopporo, near Ôsawa Parking, 5♂8♀, 20-IX-1982, NT. Sapporo-shi, Tsuneji-zawa, 1♂, 7-IX-1981, H. Ubukata. Otaru-shi, Nagahashi, Naebo area: 1 juv., 7-VIII-1992; 1♀, 1-IX-1992; 2♂, 6-IX-

1992; 2♀, 12-IX-1992, M. Ôhara, K. Sasaki, and T. Miura. Otaru-shi, from Okusawa-suigenchi to Ana-daki Falls, 1♂, 9-X-1984, NT. Hiro-o-gun, Chûrui-mura, Bansei, 1♂, 22-X-1995, Y. Kuwahara. Tokachi-gun, Urahoro-cho, Mekariishi, 1♂1♀, 22-X-1995, Y. Kuwahara. Kasa-gun, Naka-Satsunai-mura, R. Satsunai, Hachinosawa, 740 m, 1♀, 17-IX-1984, T. Kurosawa. Upper stream of R. Tottabetsu, Tottabetsu Hütte, 470 m, 11♂2♀, 13-IX-1984, A. Ohtaka. Saru-gun, Biratori-cho, Mt. Poroshiri, Nukabira-rindô, 720–750 m, 1♀, 22-VIII-1983, NT. Samani-gun, Samani-cho, Shintomi, 23-X-1995, 2♂2♀, Y. Kuwahara. Hakodate-shi, Mt. Hakodate: 120–260 m, 6♂6♀ (6♂ for chromosome observation), 8-IX-1995, NT; Yayoizaka, 100 m, 10♂8♀, 9-IX-1995, NT. Mt. Daisengen, 1♂, 15-IX-1989, N. Yasuda. AOMORI PREF. Hakkôda, Tsutanuma, 1♂, 3-XI-1990, A. Ohtaka. IWATE PREF. Mt. Iwate, Omisaka route, 950 m, 1♂1♀, 28-IX-1984, NT. Shimohei-gun, Kawai-mura, Kuzakai, Mt. Kabuto-Myôjin-dake, 4♂6♀, 760–1000 m, 29-IX-1984, NT. YAMAGATA PREF. Yamagata-shi, Mt. Zaô, from Mt. Jizô to Iroha-numa, 1510 m, 1♂, 20-VIII-1987, NT. Yonezawa-shi: Mt. Nishiazuma (Shirabu Spa), 860–1100 m, 8♂6♀, 31-VIII-1980, NT; Shirabu Spa, *Cryptomeria japonica* forest, 820–880 m, 1♂, 31-VIII-1980, NT. Nishi-Tagawa-gun, Atsumi-cho, Sekigawa, 1♂1♀, 23-IX-1989, H. Yoshida. FUKUSHIMA PREF. Urabandai, Goshikinuma, 790–830 m, 27♂10♀, 1-IX-1980, NT. Mt. Hiuchi-ga-dake: Miike, 1500–1520 m, 4♂4♀, 2-IX-1980, NT; from Miike to the summit, 1500–1700 m, 13♂13♀, 3-IX-1980, NT. GUMMA PREF. Tone-gun, Mt. Tanigawa (from Tenjindaira to Tenjin ridge), 1400–1600 m, 3♂, 28-VIII-1982, NT; Oze-ga-hara, Miharashi-Jujiro Camping-ground, 1♂, 28-VIII- 1986, A. Ohtaka. NIIGATA PREF. Minami-Uonuma-gun, Yuzawa-cho, Mt. Tairappyô: from the end of Iwanazawa forest road to Tairappyo Yama-no-ie, *Fagus crenata* forest, ca. 1200–1660 m, 1♀, 17-IX-1988,; from the summit of Mt. Tairappyô to Mt. Matsude, 1600–1983 m, 1♀, 17-IX-1988, all by A. Ohtaka.

Distribution. Sakhalin, Is. Iturup, Is. Kunashir, Hokkaido, Honshu (south to Niigata Prefecture) (Fig. 19). In Honshu, occurrence of this species seems to be limited to mountainous areas of higher altitudes.

This species is widely sympatric with *N. genufusca* in Hokkaido except for the northernmost part and mountainous areas of higher altitudes where only *N. suzukii* n. sp. is found.

Remarks. As stated above, Suzuki (1985) suggested that this species is a member of *Nelima nigricoxa* or its vicariant. However, records accumulated since that time have demonstrated that there is a wide distributional blank between the ranges occupied by *Nelima nigricoxa* Sato and Suzuki and those of the "smaller species" of *Nelima* found in northern Japan (Fig. 19). A short seminal receptacle in female ovipositor and smaller body size suggest that the "smaller species" is not a closest relative of the "larger species" namely *N. genufusca* but a vicariant of *Nelima nigiricoxa*. However, a preliminary molecular phylogenetic analysis using partial sequence of Cytochrome Oxidase I (COI) of mitochondorial DNA showed that isolated populations of "*Nelima nigricoxa*" in Kanto District may not be direct sisters to "*Nelima nigricoxa*" in southwestern Japan. Thus, genetic affiliation of the "smaller species" to main populations of *N. nigricoxa* in western Japan is also suspicious. Moreover, shiny coloration of the dorsum in adults and other diagnostic characters are rather consistent within the whole range of the "smaller species" outlined in Fig. 19. These facts favor the treatment of the "smaller species" as a distinct species *N. suzukii* n. sp.

This species is also distributed in Sakhalin Island of Russia. In the island, another species of *Nelima, N. saghalina* Roewer 1957 (Roewer 1957, p. 349), has been known to occur. However, *N. saghalina* is not conspecific with *N. suzukii* and, first of all, occurrence of *N. saghalina* in Sakhalin is dubious since no specimens of harvestmen that share characters exhibited by the male type specimen (#2878 in Senckenberg Museum, Frankfurt, seen) have been found from the island (Details are to be reported elsewhere).

Etymology. The specific epithet is named in honor of Dr. Seisho Suzuki, a pioneer of opilionid systematics in Japan and East Asia, for his contribution in establishing systematical basis for taxonomically entangled Japanese species of *Nelima*.

Acta Arachnologica Vol. 52, No. 1 掲載論文の和文要旨

ゴミグモ（クモ目：コガネグモ科）のゴミリボンが餌捕獲に及ぼす影響（pp. 1–3）

馬場友希（〒113-8657 東京都文京区弥生 1-1-1 東京大学大学院農学生命科学研究科生物多様性科学研究室）

本研究ではゴミグモ（*Cyclosa octotuberculata*）のゴミリボンが獲物の行動に影響を与え，餌捕獲数に影響を及ぼすという仮説を検証した．実験的にゴミリボンのある網と無い網を作成し，野外で餌捕獲数を比較したところ有意な差はなかった．またその他の要因を考慮にいれて重回帰分析を行ったが，餌捕獲数への影響はみとめられなかった．この結果よりゴミリボンが網上の大きな構造物にも関わらず獲物に対して視覚的効果をもたない可能性が考えられる．

札幌市近郊におけるザトウムシの季節消長と生態，およびエゾナミザトウムシとその近縁種についての分類学的ノート（pp. 5–24）

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札幌市近郊の 3 カ所（野幌，円山，北大構内）に生息するザトウムシ 11 種の季節消長と生態を調査した．ほとんどの種は年 1 化卵越冬の生活史を示したが，フタコブザトウムシ *Paraumbogrella pumilio* は年 1 化成体越冬，マキノブラシザトウムシ *Sabacon makinoi* では卵と幼体の両方での越冬が示唆された．四国に生息するザトウムシと比較すると，幼体越冬の種を欠くことが北海道産種の生活史の特徴である．卵越冬の種では，春季により早く孵化する種ほど幼体期間が長かった．また，卵越冬のほとんどの種で雌が雄よりも早く成体に達する傾向（雌先熟）がみられた．雌先熟は他のクモガタ綱や昆虫では非常に珍しいが，マザトウムシ上科 Phalangioidea のザトウムシでは一般的傾向と思われる．長い繁殖期間と雌の多数回交尾が一般的であることが雌先熟傾向を生み出しているのかもしれない．土壌性の 3 種（ブラシザトウムシ属 *Sabacon* 2 種とフタコブザトウムシ *P. pumilio*）をのぞき，どの種も幼体初期には土壌リター中で過ごすが，幼体期の途中から，草本層や樹幹へ日中の生息場所を移した．両生生殖の 3 種では性比は雄に偏る傾向がみられた．雌先熟とも関係して，性比は時間的にも変化した．7 種の産卵数と 10 種の卵サイズのデータを示した．ブラシザトウムシ科の 2 種の卵のうを初めて記録した．さらに，学名が未決定であったエゾナミザトウムシに対して *Nelima suzukii* の名称を与え，ナミザトウムシ属の分類について若干の知見を付記した．

韓国及び日本産のケムリグモ属（クモ目：ワシグモ科）数種についての分類学的検討（pp. 25–30）

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ケムリグモ属 *Zelotes* の数種について分類学的検討の結果を報告した．韓国で記載されたミカドケムリグモ *Z. kimwha* Paik 1986 と *Z. tintinnus* Paik 1986 については，同一地点から採集された雌雄の標本を検討した結果，後者を前者の新参異名とした．北海道に分布するコブシケムリグモ *Z. hayashii* Kamura 1987 とビフカケムリグモ *Z. bifukaensis* Kamura 2000 については，前者の雌雄及び後者の雄のみが知られており，後者の雌は未知であったが，新たな標本を検討した結果，従来コブシケムリグモの雌とみなされていたものは正しくはビフカケムリグモの雌であることが判明し，同時に，真のコブシケムリグモの雌も見出された．沖縄産のリュウキュウケムリグモ *Z. ryukyuensis* Kamura 1999 とツヅラケムリグモ *Z. flexuosus* Kamura 1999 については，前者の雌雄及び後者の雌のみが知られており，後者の雄は未知であったが，沖縄島における再調査の結果，これら 2 種の雄の触肢の構造は互いに極めてよく似ており，リュウキュウケムリグモの雄とみなされていたものの中にツヅラケムリグモの雄が混じっていたことが判明した．

東京都青梅市の山林から発見されたササラダニ類（イカダニ科）の 1 新種（pp. 31–33）

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青梅市の北部に広がる黒沢川沿いのコナラを主とする林の林床の倒木の樹皮から,イカダニ科に属するササラダニ類の未記載種が見出されたので *Dolicheremaeus ohmensis* オウメイカダニと命名して記載した．イカダニ科の多くの種では後体部前縁に 2 対の瘤状突起があるが，本種を含めて 6 種では,その突起が 1 対しかない．その中で本種は胴感毛の柄が短く先端部が強く膨らむこと，背毛が短いものと著しく長いものの 2 群に分かれることなどによって，既知の 5 種から区別される．

日本産キシダグモ科の 2 新種および 2 新記録種（pp. 35–42）

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日本産キシダグモ科の 2 新種，*Dolomedes orion* n. sp.オオハシリグモ（新称）と *Dolomedes zatsun* n. sp.ササキハシリグモ（新称）を記載し，*Dolomedes horishanus* Kishida 1936 ヘリジロハシリグモと *Pisaura bicornus* Zhang & Song 1992 サイホウキシダグモ（新称）の 2 種を日本から新たに記録し，再記載した．また，*Dolomedes yawatai* Ono 2002 イシガキアオグロハシリグモを西表島から新たに記録した．台湾から知られていた *Dolomedes mizhoanus* Kishida 1936 はヘリジロハシリグモの新参シノニムである．